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SIZE AND POSITION OF THE FUNCTIONAL COMPONENTS OF THE SKULL.

A CONTRIBUTION TO THE KNOWLEDGE OF THE ARCHITECTURE OF THE SKULL, BASED ON DATA IN THE LITERATURE

BY

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INTRODUCTION

In a recently published discussion on the skull in a Dutch Textbook of Comparative Anatomy of the Vertebrates I expressed as my opinion (1941, pp. 245, 250) that the skull may be regarded as a complex of relatively separate functional components, sometimes detached, sometimes united to a morphological whole, but even in this case to a certain extent independent in size, relative position and grouping. In a following article I elaborated these principles (1945) [1]. In this article (1945,

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[1] This paper (published in 1945) has been written during my sojourn in the German Civil Concentration Camp at Sint Michielsgestel, where I stayed as a hostage from the 7th of August 1942 till the 19th of February 1943. The fact that it was soon made practically impossible to receive books written in English, explains the small number of those books used for this paper.

The paper now published was begun during that period too, it has been continued and brought to a provisional end during the time that I was sent into exile by the "Befehlshaber der Sicherheitspolizei und des SD für die besetzten Niederländischen Gebiete" to the small village of Otterloo, where I had to stay from the 25th of June 1943. The study of the necessary literature for this publication was made possible and easy to me thanks to the help of my former assistant Miss J. J. P. ZAAIJER at Leiden. When this period of my life ended on the 5th of May 1945 by the liberation of our country and I returned to my work in Leyden University, I had to decide about the destiny of this manuscript. Knowing that it would be impossible to find time enough in the next few years to add many other facts from literature and from original own investigations, I decided to publish it in its present condition. As it is now it may be of much use for students in this interesting field of study. My cordial thanks are due to Dr L. D. BRONGERSMA, Dr G. C. A. JUNGE and Dr F. P. KOUMANS of the Rijksmuseum van Natuurlijke Historie at Leiden pp. 35/36) has been substantiated, that also in the skull three kinds of components can be distinguished: 1° those with a well-nigh absolutely individual shape and size ("Eigenraum"); 2° components in which this individual shape and size shows the influences of the environment; 3° components devoid of any specific shape and size: the padding elements among which may be counted pneumatic and spongy bone matter.

Size should be distinguished as absolute and relative. The relative size with regard to other surrounding cranial parts is essential for the relative position and grouping of the cranial parts. In special cases both absolute size and relative size with regard to other than the aforesaid parts, as for instance with regard to the entire skull, with regard to the size of the head and of the body size should not be overlooked.

When determining the size of a certain component or element and in judging the data in literature it should be clearly stated whether they are based on the cubic content or on the size of the surface in a level plane *e.g.* in the sagittal plane. M. SCHMIDT, according to STRATZ (1904, p. 85), determined the cubic content by filling up the cavities with wax, which was liquefied out of it later on. STRATZ (1904, pp. 85/86) himself – following up the methods for determining the size of the median section by CUVIER and TOPINARD – determined the surface of a level plane, namely the skull seen in the norma lateralis and also in the norma frontalis. STRATZ calculated the content from the largest extension of the surface in the norma frontalis and the average sagittal diameter of the norma lateralis, as if the cerebral skull and the facial skull were cylindrical bodies; he, however, dit not determine this content by a direct method (STRATZ, 1904, pp. 86–88). STRATZ restricts himself to surface sizes in the norma lateralis; he thinks, that the differences in width in dolichocephalic and brachycephalic skulls are sufficiently expressed in their

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who gave me the correct genus and species names used in this paper. At the same time I wish to thank those who made the drawings for this paper, and to Prof. H. BOSCHMA and Dr K. W. DAMMERMAN, who allowed me to choose a number of drawings out of their collections for the use as illustrations for this paper. My cordial thanks are due to Mrs J. E. WISSENBURGH-RAVENSTEIJN, Mrs M. M. HAGEMAN-BOON and Miss A. B. BAUDUIN, who translated the manuscript, and to Dr KAATJE SCHIJFSMA for the valuable help in the technical aspects. Also in the postwar period Miss J. J. P. ZAAIJER was a most valuable help to me, now in preparing this manuscript for the press.

lateral aspect owing to the correlation of the cranial parts (STRATZ, 1904, p. 87). Though this may prove to be true for one single species examined in this respect, we are not justified to replace the cubic content by the surface in a special plane or aspect without further verification, at least not when the animals compared are not closely related. As an example I only mention two beaks of birds which agree in length and height, but differ in width, one being narrow, the other wide.

In skulls of various species of animals the position of a special component which has the same absolute size in all these skulls, may be similar or different with regard to surrounding elements; if the absolute size differs, the position with respect to the surrounding elements will be different, unless the surrounding elements have decreased or increased proportionately.

When we compare functional units, that is to say analogical formations, in different skulls, we must always bear in mind that though they may be homologous, this needs by no means be the case. For they may be not homologous or not completely so. And if they are not strictly homologous, this may be due to the addition of new elements from the surroundings. In principle the component has increased in this instance; actually this need not be the case.

The functional unit comes first in our discussion. For in this paper I want to consider the skull as a "cubic jig-saw puzzle", not of morphological units, but of functional components.

Now I will discuss successively the functional units distinguished by me (1945, pp. 31/32) with regard to their absolute size, their relative size and their position with respect to the surrounding functional units; the question of the homology or non-homology will only briefly be dealt with.

1. CEREBRAL CAPSULE

a. Introduction

This chapter concerns the size and position of the cerebral capsule, that is the thin plate or layer of bone lining the cavity in the skull for the brain.

As I already discussed in a previous paper (1945, pp. 28–31), the exterior surface of the cerebral skull is not always a proof for the size of the cerebral capsule. In this connection I pointed out a number of phenomena: 1. in the first place the fact that an element (squamosum, parietale) sometimes, though lying against the cerebral skull, does not contribute to the lining of the cranial cavity for the brain; 2. the locally thickened wall in the labyrinth region; 3. thirdly it was pointed out, that sometimes the entire wall of the cranial cavity for the brain is very thick. This thickening can be solid, spongy or pneumatic. I should like to illustrate this with some data from literature. In † *Dinornis* with a relatively very small cranial cavity for the brain the skull has "expanded to the requisite extent for muscular and other attachments by a thick pneumatic cellular diploë between the outer and inner tables", which also occurs in Striges (OWEN, 1866 II, pp. 61/62). According to OWEN (1866 II, p. 438) conditions in the Proboscidea (see my fig. 1) are as follows: "The cranial much exceeds the facial part in size: its upper part forms an expanded dome: but a section, ..., shows that the cavity for the brain occupies but a small proportion of the back part of the dome's base: the rest being formed by air-sinuses, bounded by plates of bone, extending between the remote outer and inner 'tables' in the form of sinuous plates so disposed as to give greatest strength with least material". In *Giraffa camelopardalis* (L.) the vertical extent of these sinuses equals that of the cranial cavity for the brain itself (OWEN, 1866 II, p. 477, fig. 326). KINGSLEY is right when he concludes (1925, p. 186): "Cranial parts predominate over facial in higher groups, this is not always caused by brain development, for it also occurs in elephants, Ruminants and Edentates as the result of cavities in the bones". As an example of a local thickening of the cerebral skull may be mentioned the † Stegosauridae, where the frontalia and parietalia have extraordinarily increased in thickness (VERSLUYS, 1936, p. 796). In *Chimaera* the noticeably widened canalis praeorbitalis, which is placed dorsally with respect to the rostral part of the cranial cavity for the brain, causes it to appear much higher and wider than the cranial cavity for the brain really is (HOLMGREN & STENSIÖ, 1936, p. 338). A narrowing of the cranial cavity for the brain is found in the base of the cerebral skull of Crossopterygii. Here we find a fossa subchordalis ("Subchordalgrube") in the base of the otical and occipital regions, which causes the cranial cavity for the brain to be placed very far above the ventral plane of the endocranium in these two regions (HOLMGREN & STENSIÖ, 1936, pp. 351, 353). Similar conditions are found in *Dermochelys*, where in the region of the basisphenoid a plate of cartilage separates the cranial cavity for the brain from a pair of basally situated, flat, canal-like cavities (VERSLUYS, 1936, p. 800).

In principle we may deduce data as to the size of the cerebral capsule also from data concerning the volume of the brain.

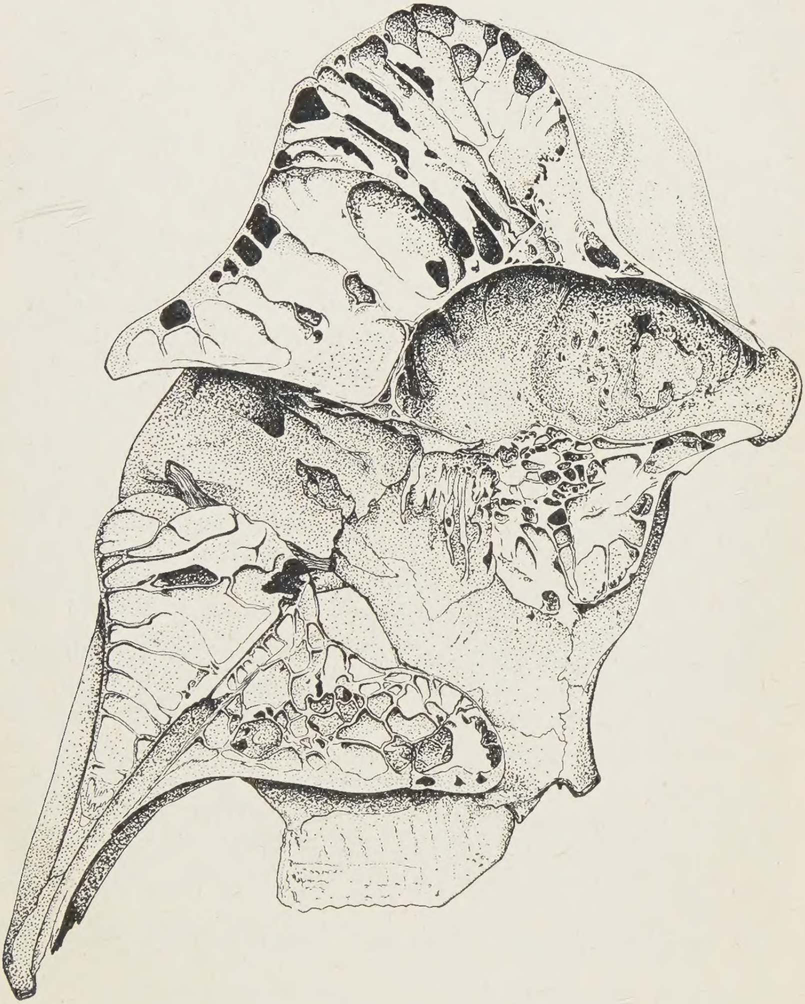

Fig. 1. *Elephas indicus* L. Left half of the skull seen from the right side in mirror image. Coll. Zool. Lab. Amsterdam. 0.15×. Original drawing by Miss W. NADORT.

b. The connection between the size of the cerebral capsule and the volume of the brain

The volume of the brain is only then a standard for the size of the cerebral capsule, when the brain fills the capsule entirely of nearly entirely.

This is the case in Aves and Mammalia. In these classes, especially in the Mammalia, this expresses itself in the so-called impressiones on the interior surface of the cerebral capsule, which impressiones sometimes give a much detailed, in other cases only an approximate and more vague impression of the relief of the brain. Further, the space between the different parts of the brain in both these classes is indicated in corresponding ridges on the inner surface of the capsule, by which the cavity in the capsule is roughly, superficially subdivided. Especially in Mammalia, even the exterior surface of the cerebral skull can be an approximate indication of the exterior surface of the principal parts of the brain. All this is connected with the fact that in Aves and Mammalia the brain practically fills the whole of the cranial cavity. In the Mammalia this is simply due to the strong development of the brain; in Aves the fact, that the position of the very large eyes restricts the space for the brain, while at the same time the skull of the Aves is laterally compressed also contributes to this effect (HALLER VON HALLERSTEIN, 1934, pp. 16, 130, 155, 167; ARIËNS KAPPERS, 1934, p. 463). In Aves this expresses itself even in the so-called impressio bulbi oculi in the wall of the brain.

Now this impressio bulbi oculi also occurs in the Reptilia, at least in most Reptilia (HALLER VON HALLERSTEIN, 1934, pp. 15, 162, 168). As for the remaining surface, the brain of the Reptilia does not fill the cerebral capsule to the same extent as in the Aves, so that the interior relief of the cerebral capsule in the Reptilia does not give an indication of the exterior surface of the brain, though roughly speaking the cerebral capsule may lie close upon the brain (HALLER VON HALLERSTEIN, 1934, pp.15, 160, 167, 204, 315).

In the Cyclostomata, Pisces and Amphibia [1]) the brain lies in a very wide cerebral capsule (HOLMGREN & STENSIÖ, 1936, pp. 439, 456, 472, but see also pp. 376, 391). This occurs both in Plagiostoma and Amphibia, where the skull is dorsoventrally depressed and where we find a wide space on either side of the brain, especially when the eyes are small, as is the case in Rays; the same holds good for the Teleostei where notwithstanding the lateral compression of the skull and the largeness of the eyes a considerable space is found round the brain (HALLER VON HALLERSTEIN, 1934, pp. 16, 150, 154/155, 204, 312, 315). Locally there is room left between brain and cerebral capsule in *Polydon*, *Acipenser*, *Amia*, *Lepisosteus*, where the so-called "myelencephalic gland" lies (HALLER VON HALLERSTEIN, 1934, p. 315). According to HOLMGREN & STENSIÖ (1936, pp. 376, 391) the brain of *Neoceratodus* and *Polypterus* should almost or fairly completely fill the cerebral capsule.

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[1]) For the relation between the size of the brain and that of the endocranial casts of some living and fossil Amphibia see: A. S. ROMER & T. EDINGER (1942), J. comp. Neurol. **77**, pp. 355-389. (Postwar addition in the manuscript)

During the embryonic or larval life – also of Pisces and Amphibia – the brain entirely fills the available space, either because the brain, which grows very fast in these early stages, has developed relatively freely, or because it has to fit into a restricted space of the skull or the head (HALLER VON HALLERSTEIN, 1934, pp. 15, 16, 150, 154, 155). In later ontogenetic stages the brain of Pisces and Amphibia stays behind in growth and the head and skull grow relatively much faster; hence the brain of the adult animal lies in a much too large cerebral capsule. OWEN (1866 I, p. 249) explains this for Pisces as follows: the brain stays behind in growth as compared with the cranial cavity for the brain, which grows at the same rate as the skull and the head, which must be large to meet and overcome the resistance of the water of the environment.

c. The size of the brain

When we now pass on to the discussion of the size of the brain in so far as it is of importance for our purpose, we shall mainly restrict ourselves to those reliable data which E. DUBOIS has stated, has cited and has used. For DUBOIS (1897 *a*, pp. 5/6, 29/30; 1897 *b*, pp. 339/340, 364; 1897 *c*, pp. 3, 20; 1913, p. 593; 1914 *a*, p. 647; 1914 *b*, p. 323; 1938, p. 38) makes a special point of having the weight of the brain determined; the weight has to be measured from fresh brain; it has to be fixed from adult and fully developed specimens by choosing only adult and full-grown individuals, in other words, the age of the individuals has to be determined or must be known; the individuals should be in good feeding-condition; one should choose if possible specimens living in wild state or at least without any obvious after-effects of their living in captivity; the average has to be determined from the largest possible number of data per species *etc.* or if it is not possible to take averages one should choose individuals representing the norm; if possible the determinations should be made for both sexes separately.

According to Dubois (1897 *a*, pp. 5/6; 1897 *b*, pp. 339/340; 1897 *c*, pp. 2/3; 1938, pp. 42, 43) therefore, many older data are of no value, because too little attention was paid to these points, especially to the stage of development and to the age. It is, however, not simple to meet these requirements. For example, even for *Homo* it is not easy to tell whether the material used was full grown or not (Dubois, 1898, p. 424). *Homo sapiens* L. is, properly speaking, the only species of which numerous data are at our disposal so that the determination of real averages is possible (Dubois, 1898, p. 423); a great many data about *Homo*, however, give too low weights of the brain, because they have been determined from individuals that died of disease and were reduced in weight (Dubois, 1919 *c*, p. 713; 1919 *d*, p. 850) [1]. The nutritive condition indeed affects the weight of the brain, though not nearly so much as the weight of the body, because emaciation reduces the weight of the brain little in contrast with the weight of the body (Dubois, 1897 *a*, p. 41; 1897 *b*, pp. 375/376; 1897 *c*, p. 27). The accurate determination of the weight of the brain meeting the aforesaid requirements is so difficult, that Dubois (1924 *a*, p. 320; 1924 *b*, p. 431; 1938, p. 39) says, that the cranial capacity is often a better measure of the brain quantity of a mammal species than the brain quantity directly determined. This can be calculated with sufficient accuracy from the capacity of the cranium, and does not appreciably differ from the former in small skulls. Very reliable characteristics are to be found in the skull for the determination, whether the specimen is really adult or not.

In the following we shall restrict ourselves to that which is to be found in Dubois' papers. Only here and there we shall add other data.

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[1] For the variation in the weight of the human brain see: F. W. & E. M. Appel (1942), Human Biol. **14**, pp. 48–58, 235–250. (Postwar addition to the manuscript)

The absolute size of the brain

The following data about the absolute weights of the brain have been classified by me according to increasing value. When Dubois states more than one value, then I have mentioned the earlier values within parentheses behind the values lastly given by Dubois. An asterisk to the species name denotes that the species in question also occurs somewhere else in the undermentioned list (different races, sexes and the like).

Of the class of the Pisces Dubois (1913, p. 600; 1914 *a*, p. 654; 1914 *b*, p. 333) mentions the absolute weight of the brain for the following species:

Gasterosteus aculeatus L. 0.022 gr;
Gobio gobio (L.) (*Gobio fluviatilis*) 0.159 gr;
Perca fluviatilis L. 0.162 gr;
Anguilla anguilla (L.) 0.170 gr;
Carassius carassius (L.) (*Carassius vulgaris*) 0.470 gr;
Conger conger (L.) (*Conger vulgaris*) 1.050 gr;
Cyprinus carpio L. 1.270 gr;
Esox lucius L. 4.860 gr.

Of the class of the Amphibia Dubois (1913, p. 599; 1914 *a*, p. 653; 1914 *b*, p. 332) gives the following data about the absolute brain weight:

Triturus cristatus (Laur.) (*Triton cristatus*) 0.019 gr;
Alytes obstetricans (Laur.) 0.041 gr;
Hyla arborea (L.) 0.043 gr;
Salamandra salamandra (L.) (*Salamandra maculosa*) 0.047 gr;
Bufo bufo (L.) (*Bufo vulgaris*) 0.073 gr;
Rana temporaria L. (*Rana fusca*) 0.088 gr;
Rana esculenta L. 0.106 gr;
Rana pipiens Schreber (*Rana virescens*) 0.153 gr;
Rana catesbeiana Shaw (*Rana Catesbyana*) 0.204 gr.

Of the class of the Reptilia Dubois gives (1913, p. 598; 1914 *a*, p. 652; 1914 *b*, p. 331):

Anguis fragilis L. 0.037–0.039 gr;
Hemidactylus brookii Gray (*Hemidactylus Brooki*) 0.043 gr;
Lacerta agilis L. 0.076 gr;
Lacerta viridis (Laur.) 0.093 gr;
Vipera berus (L.) 0.105 gr;
Testudo hermanni Gmel. (*Testudo graeca* auct. non L.) 0.360 gr;
Naja melanoleuca Hallow 0.646 gr;
Varanus niloticus (L.) 2.440 gr.

Of the class of the Aves Dubois mentions (1914 *b*, p. 329; 1919 *c*, pp. 715, 716; 1919 *d*, pp. 852, 853) the absolute weight of the brain for the following species:

Phylloscopus collybita (Vieill.) (*Phylloscopus rufus*) 0.320 gr;
Regulus regulus (L.) 0.357 gr;
Troglodytes troglodytes (L.) (*Anorthura troglodytes*) 0.488 gr;
Erithacus rubecula (L.) 0.630 gr;
Parus major L. 0.865 gr;
* *Passer domesticus* L. ♀ 0.959 gr;
* *Passer domesticus* L. ♂ 0.994 gr;
* *Colinus virginianus* (L.) ♂ 1.223 gr;
* *Colinus virginianus* (L.) ♀ 1.242 gr;
Turdus merula L. 1.80 gr;
Columba livia (L.) dom. 1.97 gr;
Anas querquedula L. 2.83 gr;
Pica pica (L.) (*Pica rustica*) 2.94 gr;
Sterna hirundo L. 3.10 gr;
* *Gallus gallus* (L.) dom. ♀ 3.24 gr;
Psittacula krameri (Scop.) (*Palaeornis docilis*) 3.58 gr;
Falco tinnunculus L. 3.74 gr;
* *Gallus gallus* (L.) dom. ♂ 3.75 gr;
Phasianus colchicus L. 3.95 gr;
Garrulus glandarius L. 3.99 gr;
Athene noctua (Scop.) 4.36 gr;
Coloeus monedula (L.) (*Corvus monedula*) 5.56 gr;
Pavo cristatus L. 5.71 gr;
Anas platyrhyncha L. (*Anas boschas*) 6.30 gr;
Larus argentatus Pont. 6.33 gr;
Amazona amazonica (L.) (*Chrysotes amazonicus*) 7.83 gr;
Buteo buteo (L.) (*Buteo vulgaris*) 7.92 gr;
Corvus corone L. 8.43 gr;
Corvus cornix L. 8.46 gr;
Cygnus olor (Gm.) 15.50 gr;
Aquila chrysaëtos (L). 18.60 gr.

Of the class of the Mammalia Dubois (1897 *a*, pp. 13, 31, 33, 36–38, 39; 1897 *b*, pp. 347, 365, 368, 370–373, 374; 1897 *c*, pp. 8, 20, 22, 24–25, 26; 1898, pp. 426, 437; 1914 *b*, pp. 326/327, 347 foot note; 1919 *a*, pp. 516 foot note, 519; 1919 *b*, pp. 724 foot note, 727; 1919 *c*, pp. 714, 717, 719, 720; 1919 *d*, pp. 851, 854, 856, 857; 1920 *b*, p. 626 foot note; 1920 *c*, p. 668 foot note; 1921, pp. 1000, 1001, 1002, 1004; 1922 *a*, pp. 1284, 1286, 1288; 1922 *b*, pp. 312, 315, 316, 320 foot note; 1922 *c*, pp. 316, 317, 320; 1923; pp. 235, 238, 239, 242 foot note, 243 foot note; 1930, pp. 252, 267, see Corrigenda; 1934 *a*, p. 186; 1938, pp. 44, 45) gives the following statements of absolute brain weight:

Sorex araneus L. (*Sorex vulgaris*) or *Sorex minutus* L. 0.125 gr;
Pippestrellus pipistrellus (Schreb.) (*Vesperugo pipistrella*) 0.150 gr;
Crocidura russula (Herm.) (*Sorex araneus* L.?) 0.17 gr;
Rhinolophus ferrum-equinum (Schreb.) ♀ 0.350 gr;

Mus musculus L. ♀ 0.43 gr;
Myotis myotis (Borkh.) (*Vespertilio murinus* Schreber) ♀ 0.445 gr;
Crocidura schweitzeri Ptrs. 0.545 gr;
* *Talpa europaea* L. ♀ 0.936 gr;
* *Talpa europaea* L. 0.962 gr;
Scotophilus gigas Dobson 1.046 gr;
Eliomys quercinus (L.) 1.25 gr;
Rattus rattus (L.) (*Mus rattus*) 1.59 gr;
Jaculus hirtipes (Licht.) (*Dipus hirtipes*) 1.85 gr;
Mustela nivalis L. (*Mustela vulgaris*) 1.95 gr;
Rattus norvegicus (Berkenhout) (*Epimys norvegicus* = *Mus decumanus* Pallas) ♂ 2.36 gr;
Tupaia javanica Horsf. ♂ 2.54 gr;
* *Erinaceus europaeus* L. ♀ 3.15 gr;
* *Erinaceus europaeus* L. 3.38 gr;
Sciurus hudsonicus (Erxl.) 4.1 gr (earlier statement 4.103 gr);
Epomophorus gambianus (Ogilby) 4.33 gr;
Dasyurus maculatus (Kerr) 5.35 gr;
* *Sciurus vulgaris* L. ♀ 6 gr;
* *Sciurus vulgaris* L. 6.10 gr;
Didelphis marsupialis L. ♂ 6.5 gr;
Sciurus carolinensis Gm. 7.58 gr;
Putorius putorius (L.) (*Mustela putorius*) ♀ 7.8 gr;
Callithrix jacchus (L.) (*Hapale jacchus*) 8 gr (earlier statement 7.97 gr);
Nycticebus coucang (Bodd.) (*Nycticebus tardigradus* L.) ♂ 8.18 gr;
Lagostomus trichodactylus Brookes 8.8 gr;
* *Oryctolagus cuniculus* (L.) (*Lepus cuniculus* L.) ♀ ferus 8.9 gr;
* *Oryctolagus cuniculus* (L.) (*Lepus cuniculus* L.) 9.3 gr;
* *Oryctolagus cuniculus* (L.) (*Lepus cuniculus* L.) ♂ ferus 9.7 gr;
Pteropus vampyrus (L.) (*Pteropus edulis* Geoffr.) ♂ 10.6 gr;
Ratufa bicolor (Sparrm.) (*Sciurus bicolor* Sparrm.) ♂ 12 gr;
Trichosurus vulpecula fuliginosus Ogilby 12.27 gr;
Leontocebus rosalia (L.) (*Midas rosalia* L.) ♀ 12.8 gr;
Manis javanica Desm. 13 gr;
Tragulus javanicus Osbeck ♂ 15.85 gr;
Lepus timidus L. 16.7 gr;
Genetta genetta (L.) (*Viverra genetta*) 17.5 gr;
Paradoxurus hermaphroditus musanga (Raffl.) 22 gr;
Saimiri sciureus (L.) (*Chrysothrix sciurea*) 24 gr;
* *Felis catus* L. (*Felis domestica* Gm.) ♀ 27 gr;
Fennecus zerda (Zimm.) (*Canis zerda*) 27.9 gr (earlier statement 25 gr);
* *Felis catus* L. (*Felis domestica* Gm.) ♂ 29 gr (earlier statement 31 gr);
* *Felis catus* L. (*Felis domestica* Gm.) run wild 34 gr;
Meles meles (L.) (*Meles taxus*) 34 gr;
† *Phenacodus primaevus* Cope about 35 gr;
Castor canadensis Kuhl 35.6 gr;
Cephalophus (*Guevei*) *maxwellii* (Ham.Sm.) 38 gr;
Civettictis civetta (Schreb.) (*Viverra civetta* Schreb.) ♂ 42.1 gr;
Lutra lutra (L.) (*Lutra vulgaris*) 47.1 gr;
Alouatta seniculus (L.) (*Mycetes seniculus*) ♂ 50 gr;

Vulpes vulpes (L.) (*Canis vulpes*) 52 gr (earlier statement 46 gr);
Alouatta ursina (Humb.) (*Mycetes ursinus*) ♀ 54 gr;
Thos aureus (L.) (*Canis aureus*) 57.1 gr (earlier statement 73 gr);
* *Canis familiaris* L. "toy-terrier", "Zwergpinscher" 58.1 gr;
Trachypithecus obscurus (Reid) (*Trachypithecus* (*Semnopithecus*) *obscurus*) 67.8 gr;
* *Trachypithecus pyrrhus* (Horsf.) (*Presbytes* (*Semnopithecus*) *maurus* F. Cuv.) ♀ 67.91 gr;
**Canis familiaris* L. lappon. ♂ 70 gr;
Macaca ira (F. Cuv.) (*Macacus cynomolgus* L.) ♂ 71 gr (earlier statement 72 gr);
* *Trachypithecus pyrrhus* (Horsf.) (*Presbytes* (*Semnopithecus*) *maurus* F. Cuv.) 71.8 gr;
Hydrochoerus hydrochaeris (L.) (*Hydrochoerus capybara* Erxl.) 75 gr;
* *Canis familiaris* L. ♀ average of small specimens 77 gr;
Presbytis melalophus (Raffl.) (*Presbytes* (*Semnopithecus*) *melalophus*) 77.3 gr;
* *Trachypithecus pyrrhus* (Horsf.) (*Presbytes* (*Semnopithecus*) *maurus* F. Cuv.) ♂ 77.31 gr (earlier statement 70 gr);
Myrmecophaga jubata L. 84 gr;
Hylobates lar mulleri Martin (*Hylobates mulleri*) 86.1 gr;
* *Canis familiaris* L. average of numerous specimens of various sizes 89 gr (earlier statements 85.33 and 87 gr);
† *Uintatherium mirabile* (Marsh) (*Dinoceras mirabile*) 92 gr;
Hylobates lar agilis F. Cuv. (*Hylobates agilis*) 93.3 gr;
Hylobates lar leuciscus Geoffroy (*Hylobates leuciscus* Kuhl) ♀ 94.5 gr;
Ateles geoffroyi Kuhl 95.5 gr;
Hylobates lar (L.) 96.4 gr;
* *Canis familiaris* L. ♂ average of large specimens 100 gr;
Canis nubilus Say 115.5 gr;
* *Canis familiaris* L. Bernh. ♂ 123 gr;
Capra hircus L. 124 gr;
Cebus capucinus (L.) 125 gr;
* *Ovis aries* L. ♀ mean 125 gr;
Hylobates syndactylus (Desm.) or *Symphalangus syndactylus* (Desm.) (*Symphalangus* (*Hylobates*) *syndactylus* Desm.) ♀ 130 gr;
Lycaon pictus (Temm.) ♂ 131 gr;
* *Canis familiaris* L. Leonb. 135 gr;
Puma concolor (L.) (*Felis concolor* L.) ♂ 137.5 gr;
* *Ovis aries* L. ♂ mean 140 gr;
Canis lupus L. 147.6 gr (earlier statement 139 gr);
Tapirus terrestris (L.) (*Tapirus americanus* L.) ♂ 169 gr;
Panthera leo (L.) (*Felis leo* L.) ♂ 219 gr;
Phoca vitulina L. 266.5 gr;
Oryx beisa (Rüpp.) ♂ 280 gr;
Panthera tigris (L.) (*Felis tigris*) 291 gr;
* *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) ♂ 325 gr;
Zalophus californianus (Less.) (*Otaria californiana*) 374.5 gr (earlier statement 399 gr);
Equus (*Asinus*) *asinus* L. ♂ 385 gr;
* *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) ♀ 385.5 gr;
Pongo pygmaeus (Hopp.) (*Simia satyrus* auct. non L.) ♂ 400 gr;
* *Bos taurus* L. dom. 400–450 gr (earlier statement 350 gr);

Alces americana (Clinton) 407 gr;
Gorilla gorilla (Savage & Wyman) 426.25 gr;
* *Bos taurus* L. dom. ♀ mean 429 gr;
* *Bos taurus* L. dom. ♂ mean 480 gr;
Phocaena phocoena (L.) (*Phocaena communis*) 512 gr;
Equus caballus L. 532 gr (earlier statement 615 gr);
Hippopotamus amphibius L. 582 gr;
Camelus dromedarius L. 650 gr;
Giraffa camelopardalis (L.) (*Camelopardalis giraffa* Schreb.) ♂ 680 gr;
† *Pithecanthropus erectus* (Dubois) 829–850 gr;
* *Homo sapiens* L. ♀ European average 1220 gr (earlier statements 1224 gr and 1235 gr);
* *Homo sapiens* L. average 1353 gr (earlier statement rather more than 1400 gr);
* *Homo sapiens* L. ♂ European average 1360 gr (earlier statements 1431 gr and 1375 gr);
Tursiops truncatus (Mont.) (*Tursiops tursiops*) ♀ 1886 gr;
Elephas indicus L. ♂ 5443 gr;
Sibbaldus musculus (L.) or *Balaenoptera physalus* (L.) (*Balaenoptera musculus*) 6700 gr;
Balaenoptera Sibbaldi Gray (probably *Sibaldus musculus* (L.)) 12000 gr (earlier statement 7000 gr).

In the above mentioned series of data only a few fossils occurred. Concerning them we may add that according to MARSH(see DUBOIS, 1897 *a*, pp. 3/4; 1897 *b*, p. 337; 1897 *c*, p. 1; 1928 *a*, p. 254; 1928 *b*, p. 307; see also HALLER VON HALLERSTEIN, 1934, pp. 22/23): 1. "All Tertiary mammals had small brains"; 2. "There was a general increase in the size of the brain during this period"; 3. "This increase was confined mainly to the cerebral hemispheres, or higher portions of the brain". DUBOIS (1928 *a*, pp. 254, 255; 1928 *b*, p. 308) remarks that it is mainly due to the underrating of the effect of the body size, which will be discussed later, that the first two articles, drawn up by O. C. MARSH, are not valid. Not all the Tertiary Mammals had small brains and many species from the Upper Tertiary are not inferior, as regards the size of the encephalon, to the recent species. Nor has the increase of the size of the brain during the Tertiary period been general. In the lowest cephalised Mammalia of the present day (Insectivora, Chiroptera) such an increase has not taken place. In the third article according to DUBOIS the word "mainly" has to be dropped, for the increase in size was exclusively confined to the cerebral hemispheres, the prosencephalon. We may add, that according to MARSH the same would have taken place for the Sauropsida during the Jurassic period; afterwards this was contradicted for the Reptilia (HALLER VON HALLERSTEIN, 1934, pp. 22/23).

Among the fossil Mammalia the very striking smallness of the cerebrum in † Amblypoda is well-known (Dubois, 1930, p. 271).

In the above series of data those concerning *Homo sapiens* L. no doubt refer to Europeans, also when this is not expressly mentioned. According to Dubois (1898, p. 441) the brain weight is 5–10 % less for coloured human races.

We can gather from the series of data that Man is surpassed by some large Mammalia in absolute brain weight. Dubois (1897 *a*, pp. 4, 20; 1897 *b*, pp. 338, 354; 1897 *c*, pp. 2, 12; 1922 *b*, p. 309; 1923, p. 232) emphatically points out, that *Homo* is only surpassed in absolute weight of the brain by *Elephas* (nearly 4 ×), the largest Cetacea (positively 5 ×) and by *Hydrodamalis gigas* (Zimm.) (*Rhytina Stelleri*) (1½ ×); of these the largest whale species is a thousand times heavier than Man.

When we survey the absolute weight of the brain in all classes of the Vertebrata, we must conclude with Dubois (1913, p. 597; 1914 *a*, p. 651; 1914 *b*, p. 328) that the weight of the brain descends in the Pisces, Amphibia and Reptilia, both absolutely and relatively (see beneath), as low as to the order of magnitude of about 10 % of that of the Aves and Mammalia. Among the Reptilia we have to make an exception for the † Theromorpha in which – as in the Aves and Mammalia – the size of the brain both absolutely and relatively is large.

The relative size of the brain

Passing on to the discussion of the relative size of the brain, we must first establish the fact, that the data most valuable to our purpose are wanting. For these would be statements about the relation of the brain to the data (length, weight, volume *etc.*) of the skull or the head. In Dubois' historical survey of the literature and in his own investigations the size of the brain is only mentioned in relation to that of the spinal cord, the length of the body, the surface of the body, but especially to the weight of the body.

As to the spinal cord it may be mentioned that the brain weight in *Homo sapiens* L. amounts to 50 × the weight of the spinal cord, in *Canis familiaris* L. ¹) and *Felis catus* L. (*Felis domestica* Gm.) 3 to 4 or 5 ×, in *Equus caballus* L. 2½ × and in *Oryctolagus cuniculus* (L.) (*Lepus cuniculus* L.) 2 times. Man is second to all Mam-

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¹) See also: H. B. Latimer (1942), Growth **6**, pp. 39–57. (Postwar addition to the manuscript)

malia as to the weight of the spinal cord (DUBOIS, 1897 *a*, p. 20; 1897 *b*, p. 354; 1897 *c*, p. 12).

The length of the body is also thought to be connected with the measure for the quantity of the brain (DUBOIS, 1913, p. 594; 1914 *a*, pp. 648/649; 1914 *b*, p. 324). Restricting ourselves to individuals of one species it was found for *Homo sapiens* L., that the weights of the brain stand in the relation of the lengths of the body raised to a power of 0.6734 on an average, so to a number far below 1 (DUBOIS, 1898, pp. 438/439/440). When determining the length of the body of cadavers, as compared with the length of the body of living individuals, a correction should be made (DUBOIS, 1898, p. 426). The weights of the brain for *Homo sapiens* L. stand in a simple relation (probably a direct proportionality is meant) to the length of head plus trunk ("im einfachen Verhältniss zu den Sitzlängen"), which is less variable than the length of the body. Only adult individuals, however, should be taken into account; for not wholly fullgrown individuals the exponent is lower than 1 (DUBOIS, 1898, pp. 439/440).

When we compare individuals of different species of Mammalia – even when we compare so-called homoneuric species (see below) – the weights of the brain do not appear to run parallel to the length of the head plus trunk. For instance the brain weight in proportion to the length of head plus trunk is 2 to 2½ times as heavy in *Pongo pygmaeus* (Hopp.) (*Simia satyrus* auct.) as in *Hylobates lar leuciscus* Geoffroy (*Hylobates leuciscus* Kuhl), idem in *Oryx beisa* (Rüpp.) as in *Cephalophus* (*Guevei*) *maxwellii* (Ham. Sm.), in *Panthera leo* (L.) (*Felis leo* L.) as in *Felis catus* L. (*Felis domestica* Gm.), in *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus* = *Mus decumanus* Pallas) as in *Mus musculus* L. (DUBOIS, 1898, p. 440).

The size of the surface of the body is also thought to be connected with the measure for the quantity of the brain. Among animals which differ considerably as to size of the body, but which in all other respects are comparable, small animals always possess more brain per unit of the body surface than large species. In this sense *Hylobates* (*Symphalangus*) *syndactylus* (Desm.) possesses 1.27 times as much brain as *Pongo pygmaeus* (Hopp.) (*Simia satyrus* auct.), *Cephalophus* (*Guevei*) *maxwellii* (Ham.Sm.) 1.37 times as much as *Oryx beisa* (Rüpp.), *Mus musculus* L. 1.40 times as much as *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus* = *Mus decumanus* Pallas) and *Felis catus* L. (*Felis domestica* Gm.) 1.51 times as much as *Panthera leo* (L.) (*Felis leo* L.), the body surface of the latter being 11 times that of the cat (Dubois, 1897 *a*, pp. 22, 28; 1897 *b*, pp. 356, 362; 1897 *c*, pp. 14, 18/19). Formerly a simple proportionality was supposed to exist between the weight of the brain and the surface of the body because of metabolism, but according to Dubois (1897 *a*, pp. 9/10; 1897 *b*, p. 343; 1897 *c*, p. 5), a relation does exist, but by no means a direct simple proportionality. Also the question arises, if there might not be a proportionality between the brain weight and the surface of the body because of the organs of sense (skin; sensorial connection with the outer world is a question of surface) or of the muscles (muscular action is a question of surface) (Dubois, 1913, p. 594; 1914 *a*, p. 648; 1914 *b*, p. 324; 1917, p. 288; 1920 *a*, p. 85; 1922 *b*, p. 310; 1923, p. 233). It is at any rate conceivable that the extension or the specification of some definite receptive surface (of sense) may determine the quantity of the brain (Dubois, 1913, pp. 594/595; 1914 *a*, p. 649; 1914 *b*, p. 324). If there exists a proportionality between the weight of the brain and the surface of the body, then in animals equal in organisation and shape, but not in size the weights of the brain must be to each other as $(\text{the length of the body})^2$ or as $\sqrt[3]{(\text{weight of the body})^2}$, that is as the weight of the body raised to the power 0.666..., while in animals not equal in organisation nor in shape yet another factor influences the relation (see also Dubois, 1897 *a*, pp. 27/28; 1897 *b*, pp. 361/362; 1897 *c*, p. 18). As we shall see later on, this so-called relation-exponent is practically always lower than 0.666..., as a simple proportionality between the weight of the brain and the surface of the body does not exist.

The relations dealt with here of the weight of the brain to the weight of the spinal cord, to the length of the body and its surface are of little value for our purpose in the stage to which the investigation has progressed and with respect to the results obtained.

The relative size of the brain as related to the weight of the body

The investigation into the relation of the weight of the brain to the weight of the body has been much more extensive and much more thorough and has led to reliable conclusions.

The particular stipulations made by Dubois for the determination of the weight of the brain also apply to the measuring of the weight of the body. We will not repeat these parallel stipulations. The numerous data about *Homo sapiens* L. tell us that the weight of the body is very variable and that therefore a norm is not easily to be fixed, for the weight of the body depends on the contents of the intestinal tract, on the quantity of fat and of water of the body and the like (Dubois, 1898, p. 438). When determining the weight of the body of a bird Dubois (1919 *c*, p. 716; 1919 *d*, p. 853) adds, that the body weight is without "ballast", *i.e.*, with emptied crop and stomach. Determinations of the body weight of animals have very seldom been made from specimens living in the wild state of nature. Specimens from zoological gardens are not always full-grown; they have mostly died of disease and are therefore too thin. The body weight of such specimens is therefore often far below the characteristic body weight; in monkeys the weight of the body has often sunk to half of the normal weight, in zoo-specimens of *Phoca vitulina* L. sometimes to 1/5 (Dubois, 1924 *a*, pp. 320, 321; 1924 *b*, pp. 431, 432; 1938, p. 38; see 1921, p. 1002 and 1922 *a*, p. 1286 on *Alouatta* (*Mycetes*)). Such data of too low weights of the body – occasionally of a too high body weight – are rejected by Dubois as useless (1919 *c*, p. 716; 1919 *d*, p. 853; 1938, pp. 42, 43). Likewise the body weights of human cadavers found after emaciation through disease (Dubois, 1898, p. 431). So the number of reliable data is small. Only in *Homo sapiens* L. many data are available and real averages can be determined (Dubois, 1898, p. 423). But the direct course to determine the normal weights of the body belonging individually to the weights of the brain is only seldom open in *Homo* and there are as yet too few data available about normal individuals that have died a sudden death and of which both brain weight and body weight have been determined per individual (Dubois, 1898, p. 424; 1913, p. 601; 1914 *a*, p. 655; 1914 *b*, p. 334; 1919 *c*, p. 713; 1919 *d*, p. 850). In *Homo* therefore two indirect courses are followed in the main: 1. by calculating the weight of the brain of living Man from the dimensions of the head according to the method of Welcker; 2. by determining directly the weight of the brain of a definite social class and determining the average weights of the bodies of Men of the same class (Dubois, 1898, p. 426; 1913, p. 601; 1914 *a*, p. 655; 1914 *b*, pp. 334/335). In fossils the weight of the body is not to be determined; sometimes it can be estimated fairly accurately on the base of the size of the skeleton in comparison with that of recent animals of which the weight of the body is known; the volume of the brain is then determined on the basis of casts of the cavity for the brain (DUBOIS, 1930, pp. 260/261).

In stages of development

The changes in the relation of the brain weight to the weight of the body during the development from the new-born animal to the adult should be considered here somewhat more thoroughly.

Generally speaking we may say that in early stages of development the brain is relatively considerably larger than in more advanced stages.

In the development of the typical teleost skull the brain becomes very large at an early stage of development according to GREGORY (1933, p. 450).

About this matter in Mammalia DUBOIS (1897 *a*, p. 5; 1897 *b*, p. 339; 1897 *c*, p. 3; 1898, p. 432; 1914 *b*, p. 330 foot note; 1917, pp. 283, 288; 1919 *c*, p. 720 foot note; 1919 *d*, p. 857 foot note; 1922 *b*, pp. 327/328; 1923, pp. 250/251) states the following. The brain attains the end of the growth much earlier than the rest of the body and therefore reaches the adult stage much earlier. Thus early in the life of the individual the brain assumes the volume of the adult state of the body. That is the reason why after birth the weight of the brain does not increase with age to the same degree as the rest of the body. *Homo sapiens* L. ♂ at the age of 9 years has already the brain volume of the adult, the same is the case with a girl of 6 years old; the weight of the body is by that time only half that of the adult [1]). A similar remark holds among others for the Dog, the Rat, the Great Ant-Eater, the Sparrow, the Chicken, the Crocodile, the Frog, the Salmon, in short for all the Vertebrata. In *Semnopithecus (Trachypithecus?)* the brain reaches its maximum weight so early that already in baby specimens it approximates the brain weight of the full-grown animal. In young animals on the whole and not only in *Homo* the brain is proportionately much larger and much heavier than when the body has reached the adult state. In *Homo sapiens* L. at birth the brain weight is 11 % of the body weight, in adult specimens 2.128 % (Haller von Hallerstein, 1934, p. 24 gives 12.6 % and 2.2 % respectively). In the "Dachshund" at birth the brain weight is 3.448 %, in the adult 0.741 %. In a specimen of *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus*) of 7 grams body weight the brain weight is less than 10 % of the body weight, whereas in a full-grown specimen the brain weight is 0.625 % of the body weight. In a specimen of the frog *Rana catesbeiana* Shaw of 4½ grams body weight the brain weight constitutes 1 % of the body weight, in a specimen of 200 grams body weight the brain weight is only 0.1 % of the body weight. This gives the skulls of them all, in their first youth, a much more humanlike appearance than they have in the adult state. So this phenomenon occurs not only in Monkeys.

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[1]) For the relation between brain weight and body weight in the ontogeny of Man see: J. ARIËNS KAPPERS (1936), Proc. Acad. Sci. Amst. **39** and J. ARIËNS KAPPERS (1943), Versl. gewone Vergad. Akad. Amst. **52**, pp. 359–372. For the same relation in a number of Primates see: F. WEIDENREICH (1941), Trans. Amer. Philos. Soc. **36**, pp. 321–442; A. H. SCHULTZ (1941) Amer. J. phys. Anthrop. **28**, pp. 273-287 and A. H. SCHULTZ (1944), Amer. J. phys. Anthrop. **2**, pp. 1-129. (Postwar addition in the manuscript)

It is evident from the determinations of weight in young individuals how great the influence of development with age is on the relative brain weight. But also other factors have a great influence, such as the coefficient of cephalisation, which we shall discuss later on; in Pisces, Amphibia and Reptilia the influence on this coefficient is not by a long way so great as in Mammalia.

In adult animals

Hereafter may follow the data about the relation of the brain weight to the body weight, determined from adult animals that meet the special requirements of Dubois and which Dubois has determined himself and those data determined by others which Dubois has judged sufficiently reliable to use them. This relation has been expressed by me in percents and the data have been arranged according to the increasing values of the percentage. When Dubois states more than one set of weights, I have mentioned the previously given values within parentheses behind the values lastly given by Dubois. An asterisk to the species name denotes that the species in question also occurs elsewhere in the undermentioned list (different races, sexes and the like). All weights in the undermentioned list have been expressed in grams, the weight of the brain coming first, that of the body second in the list.

Of the class of the Pisces Dubois (1913, p. 600; 1914 *a*, p. 654; 1914 *b*, p. 333) mentions the relation between brain weight and body weight for the following species:

Conger conger (L.) (*Conger vulgaris*) 0.010 % (1.050 in 10000);
Anguilla anguilla (L.) 0.026 % (0.170 in 650);
Esox lucius L. 0.038 % (4.860 in 12700);
Cyprinus carpio L. 0.069 % (1.270 in 1817.3);
Perca fluviatilis L. 0.241 % (0.162 in 67.27);
Gobio gobio (L.) (*Gobio fluviatilis*) 0.377 % (0.159 in 42.196);
Gasterosteus aculeatus L. 1.520 % (0.022 in 1.447);
Carassius carassius (L.) (*Carassius vulgaris*) 9.004 % (0.470 in 5.22).

Franz (1934, p. 1053) remarks that for Teleostei the brain of the Mormyridae is enormously large.

Of the class of the Amphibia Dubois (1913, p. 599; 1914 *a*, p. 653; 1914 *b*, p. 332) mentions the relation between brain weight and body weight for the following species:

Rana catesbeiana Shaw 0.083 % (0.204 in 244.4);
Bufo bufo (L.) (*Bufo vulgaris*) 0.164 % (0.073 in 44.5);
Rana temporaria L. (*Rana fusca*) 0.166 % (0.088 in 53.0);
Salamandra salamandra (L.) (*Salamandra maculosa*) 0.189 % (0.047 in 24.88);
Rana pipiens Schreber (*Rana virescens*) 0.209 % (0.153 in 73.35);
Rana esculenta L. 0.238 % (0.106 in 44.5);
Triturus cristatus (Laur.) (*Triton cristatus*) 0.255 % (0.019 in 7.46);
Alytes obstetricans (Laur.) 0.532 % (0.041 in 7.7);
Hyla arborea (L.) 0.896 % (0.043 in 4.8).

Of the class of the Reptilia Dubois (1913, p. 598; 1914 *a*, p. 652; 1914 *b*, p. 331) mentions the relation between body weight and brain weight for the following species:

Varanus niloticus (L.) 0.033 % (2.440 in 7500);
Testudo hermanni Gmel. (*Testudo graeca* auct.) 0.036 % (0.360 in 993.58);
Naja melanoleuca Hallow 0.036 % (0.646 in 1770);
Vipera berus (L.) 0.164 % (0.105 in 64.2);
Anguis fragilis L. 0.196 % (0.037 in 18.9) or 0.239 % (0.039 in 16.252);
Lacerta viridis (Laur.) 0.554 % (0.093 in 16.8);
Lacerta agilis L. 0.608 % (0.076 in 12.507);
Hemidactylus brookii Gray (*Hemidactylus Brooki*) 0.915 % (0.043 in 4.7).

Of the class of the Aves Dubois (1914 *b*, p. 329; 1919 *c*, pp. 715, 716; 1919 *d*, pp. 852, 853) mentions the relation between body weight and brain weight for the following species:

* *Gallus gallus* (L.) dom. ♂ 0.225 % (3.75 in 1664.79);
Pavo cristatus L. 0.257 % (5.71 in 2220);
Cygnus olor (Gm.) 0.292 % (15.50 in 5300);
* *Gallus gallus* (L.) dom. ♀ 0.297 % (3.24 in 1091.07);
Phasianus colchicus L. 0.324 % (3.95 in 1220);
Aquila chrysaëtos (L.) 0.353 % (18.60 in 5273);
Anas platyrhyncha L. (*Anas boschas*) 0.588 % (6.30 in 1072);
Larus argentatus Pont. 0.633 % (6.33 in 1000);

Columba livia (L.) dom. 0.729 % (1.97 in 270);
Buteo buteo (L.) (*Buteo vulgaris*) 0.784 % (7.92 in 1010);
Anas querquedula L. 0.922 % (2.83 in 307);
* *Colinus virginianus* (L.) ♂ 0.985 % (1.223 in 124.1);
* *Colinus virginianus* (L.) ♀ 1.009 % (1.242 in 123);
Sterna hirundo L. 1.127 % (3.10 in 275);
Corvus corone L. 1.505 % (8.43 in 560);
Falco tinnunculus L. 1.612 % (3.74 in 232);
Corvus cornix L. 1.692 % (8.46 in 500);
Turdus merula L. 1.915 % (1.80 in 94);
Athene noctua (Scop.) 2.096 % (4.36 in 208);
Amazona amazonica (L.) (*Chrysotes amazonicus*) 2.303 % (7.83 in 340);
Coloeus monedula (L.) (*Corvus monedula*) 2.417 % (5.56 in 230);
Garrulus glandarius L. 2.660 % (3.99 in 150);
* *Passer domesticus* L. ♂ 3.227 % (0.994 in 30.8);
Erithacus rubecula (L.) 3.316 % (0.630 in 19);
* *Passer domesticus* L. ♀ 3.341 % (0.959 in 28.7);
Pica pica (L.) (*Pica rustica*) 3.459 % (2.94 in 85);
Psittacula krameri (Scop.) (*Palaeornis docilis*) 3.978 % (3.58 in 90);
Phylloscopus collybita (Vieill.) (*Phylloscopus rufus*) 4.372 % (0.320 in 7.32);
Parus major L. 4.626 % (0.865 in 18.70);
Troglodytes troglodytes (L.) (*Anorthura troglodytes*) 5.270 % (0.488 in 9.26);
Regulus regulus (L.) 6.515 % (0.357 in 5.48).

According to HALLER VON HALLERSTEIN (1934, p. 168) we find the relatively largest and also broadest brain among Psittaci and Passeriformes.

Of the class of the Mammalia [1]) DUBOIS (1897 *a*, pp. 4, 5, 31, 33, 36-38; 1897 *b*, pp. 338, 339, 365, 368, 370-373; 1897 *c*, pp. 2, 20, 22, 24–25; 1914 *b*, pp. 326/327, 347 foot note; 1919 *a*, pp. 516 foot note, 519; 1919 *b*, pp. 724 foot note, 727; 1919 *c*, pp. 714, 717, 719, 720; 1919 *d*, pp. 851, 854, 856, 857; 1920 *b*, p. 626 foot note; 1920 *c*, p. 668 foot note; 1921, pp. 1000, 1001, 1002, 1004; 1922 *a*, pp. 1284, 1286, 1288; 1922 *b*, pp. 312, 315, 320 foot note; 1923, pp. 235, 238, 242 foot note, 243 foot note; 1922 *c*, pp. 316, 317; 1930, p. 252; 1934 *a*, p. 186; 1938, pp. 44, 45) mentions the relation between brain weight and body weight for the following species:

Balaenoptera Sibbaldi Gray (probably *Sibbaldus musculus* (L.)) 0.012 % (12000 in 100000000) (earlier statements 0.007 %: 7000 in 100000000 or 0.009 %: 7000 in 74000000);
Sibbaldus musculus (L.) or *Balaenoptera physalus* (L.) (*Balaenoptera musculus*) 0.018 % (6700 in 37385000);

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[1]) For the relation between brain weight and body weight in adult Man and other Primates see: A. H. SCHULTZ (1941), Amer. J. phys. Anthrop. **28**, pp. 273-287. (Postwar addition in the manuscript)

Hippopotamus amphibius L. 0.033 % (582 in 1755000);
* *Bos taurus* L. dom. ♂ 0.089 % (480 in 540000);
Camelus dromedarius L. 0.104 % (650 in 625000);
Tapirus terrestris (L.) (*Tapirus americanus* L.) ♂ 0.106 % (169 in 160000);
* *Bos taurus* L. dom. ♀ 0.108 % (429 in 397000);
Giraffa camelopardalis (L.) (*Camelopardalis giraffa* Schreb.) ♂ 0.128 % (680 in 529000);
Equus caballus L. 0.145 % (532 in 368000) (earlier statement 0.164 %: 615 in 375000);
Alces americana (Clinton) 0.149 % (407 in 272000);
* *Hydrochoerus hydrochaeris* (L.) (*Hydrochoerus capybara* Erxl.) 0.150 % (75 in 50000) or 0.263 % (75 in 28500);
Manis javanica Desm. 0.163 % (13 in 8000);
Panthera tigris (L.) (*Felis tigris* L.) 0.166 % (291 in 175000);
Elephas indicus L. ♂ 0.179 % (5443 in 3048000);
Panthera leo (L.) (*Felis leo* L.) ♂ 0.183 % (219 in 119500);
Castor canadensis Kuhl 0.183 % (35.6 in 19500);
Didelphis marsupialis L. ♂ 0.187 % (6.5 in 3480);
Equus (*Asinus*) *asinus* L. ♂ 0.220 % (385 in 175000);
Lagostomus trichodactylus Brookes 0.228 % (8.8 in 3854);
* *Canis familiaris* L. Leonb. 0.229 % (135 in 59000);
Tursiops truncatus (Mont.) (*Tursiops tursiops*) ♀ 0.231 % (1886; body weight 432 times as much);
* *Canis familiaris* L. Bernh. ♂ 0.232 % (123 in 53000) or 0.267 % (123 in 46000);
* *Ovis aries* L. ♀ 0.250 % (125 in 50000);
* *Ovis aries* L. ♂ 0.255 % (140 in 55000);
Oryx beisa (Rüpp.) ♂ 0.262 % (280 in 107000);
* *Hydrochoerus hydrochaeris* (L.) (*Hydrochoerus capybara* Erxl.) 0.263 % (75 in 28500) or 0.150 % (75 in 50000);
* *Canis familiaris* L. Bernh. ♂ 0.267 % (123 in 46000) or 0.232 % (123 in 53000);
Meles meles (L.) (*Meles taxus*) 0.283 % (34 in 12000);
Trichosurus vulpecula fuliginosus Ogilby (*Trichosurus fuliginosus*) 0.292 % (12.27 in 4196);
Myrmecophaga jubata L. 0.299 % (84 in 28086) (earlier statement 0.210 %: 84 in 40000);
Puma concolor (L.) (*Felis concolor* L.) ♂ 0.312 % (137.5 in 44000);
Capra hircus L. 0.331 % (124 in 37500);
* *Erinaceus europaeus* L. ♀ 0.356 % (3.15 in 885);
* *Canis familiaris* L. ♂ average of large specimens 0.364 % (100 in 27503);
Canis lupus L. 0.369 % (147.6 in 40000) (earlier statement 0.376 %: 139 in 37000);
Canis nubilus Say 0.398 % (115.5 in 29030);
Phocaena phocoena (L.) (*Phocaena communis*) 0.427 % (512 in 120000);
Lepus timidus L. 0.436 % (16.7 in 3833);
* *Erinaceus europaeus* L. 0.444 % (3.38 in 762);
Gorilla gorilla (Savage & Wyman) 0.470 % (426.25 in 90720);
* *Canis familiaris* L. average of numerous specimens of various sizes 0.494 % (89 in 18000) (earlier statement 0.503 %: 87 in 17300);

Civettictis civetta (Schreb.) (*Viverra civetta* Schreb.) ♂ 0.495 % (42.1 in 8500);
Zalophus californianus (Less.) (*Otaria californiana*) 0.506 % (374.5 in 74000) (earlier statement 0.380 %: 399 in 105000);
Lycaon pictus (Temm.) ♂ 0.516 % (131 in 25400);
Rattus norvegicus (Berkenhout) (*Epimys norvegicus* = *Mus decumanus* Pallas) ♂ 0.527 % (2.36 in 448);
Pongo pygmaeus (Hopp.) (*Simia satyrus* auct.) ♂ 0.544 % (400 in 73500);
* *Canis familiaris* L. lappon. ♂ 0.581 % (70 in 12040);
Macaca ira (F. Cuv.) (*Macacus cynomolgus* L.) ♂ 0.592 % (71 in 12000);
Phoca vitulina L. 0.618 % (266.5 in 43110, emaciated);
Crocidura schweitzeri Ptrs. 0.665 % (0.545 in 82);
* *Oryctolagus cuniculus* (L.) (*Lepus cuniculus* L.) ♂ ferus 0.683 % (9.7 in 1420);
Paradoxurus hermaphroditus musanga (Raffl.) (*Paradoxurus musanga* Gray) 0.709 % (22 in 3100);
Alouatta seniculus (L.) (*Mycetes seniculus*) ♂ 0.741 % (50 in 6750);
* *Oryctolagus cuniculus* (L.) (*Lepus cuniculus* L.) 0.759 % (9.3 in 1226);
* *Trachypithecus pyrrhus* (Horsf.) (*Presbytes* (*Semnopithecus*) *maurus* F. Cuv.) ♂ 0.766 % (77.31 in 10087.5) (earlier statement 0.795 %: 70 in 8800);
Tragulus javanicus Osbeck ♂ 0.778 % (15.85 in 2037);
Rattus rattus (L.) (*Mus rattus*) 0.795 % (1.59 in 200);
Thos aureus (L.) (*Canis aureus*) 0.835 % (57.1 in 6836) (earlier statement 0.730 %: 73 in 10000);
Pteropus vampyrus (L.) (*Pteropus edulis* Geoffr.) ♂ 0.839 % (10.6 in 1262.5);
Vulpes vulpes (L.) (*Canis vulpes*) 0.849 % (52 in 6120) (earlier statement 0.836 %: 46 in 5500);
* *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) ♀ 0.856 % (385.5 in 45020);
Ratufa bicolor (Sparrm.) (*Sciurus bicolor* Sparrm.) ♂ 0.857 % (12 in 1400);
Presbytis melalophus (Raffl.) (*Presbytes* (*Semnopithecus*) *melalophus*) 0.859 % (77.3 in 9000);
* *Oryctolagus cuniculus* (L.) (*Lepus cuniculus* L.) ♀ ferus 0.862 % (8.9 in 1032);
* *Canis familiaris* L. ♀ average of small specimens 0.864 % (77 in 8908);
* *Trachypithecus pyrrhus* (Horsf.) (*Presbytes* (*Semnopithecus*) *maurus* F. Cuv.) ♀ 0.867 % (67.91 in 7830);
* *Felis catus* L. (*Felis domestica* Gm.) ♂ 0.883 % (29 in 3284) (earlier statement 0.939 %: 31 in 3300);
* *Felis catus* L. (*Felis domestica* Gm.) run wild 0.932 % (34 in 3650);
Lutra lutra (L.) (*Lutra vulgaris*) 0.942 % (47.1 in 5000);
* *Trachypithecus pyrrhus* (Horsf.) (*Presbytes* (*Semnopithecus*) *maurus* F. Cuv.) 0.970 % (71.8 in 7400);
* *Talpa europaea* L. 1.013 % (0.962 in 95);
Scotophilus gigas Dobson 1.036 % (1.046 in 101);
Trachypithecus obscurus (Reid) (*Trachypithecus* (*Semnopithecus*) *obscurus*) 1.037 % (67.8 in 6540);
* *Talpa europaea* L. ♀ 1.069 % (0.936 in 87.5);
* *Felis catus* L. (*Felis domestica* Gm.) ♀ 1.120 % (27 in 2410);
Cephalophus (*Guevei*) *maxwellii* (Ham. Sm.) 1.132 % (38 in 3357);
Genetta genetta (L.) (*Viverra genetta*) 1.167 % (17.5 in 1500);
Dasyurus maculatus (Kerr) 1.274 % (5.35 in 420);
Putorius putorius (L.) (*Mustela putorius* L.) ♀ 1.315 % (7.8 in 593);
Hylobates lar (L.) 1.329 % (96.4 in 7250);

Myotis myotis (Borkh.) (*Vespertilio murinus* Schreber) ♀ 1.336 % (0.445 in 33.3);
Hylobates (*Symphalangus*) *syndactylus* (Desm.) ♀ 1.368 % (130 in 9500);
Fennecus zerda (Zimm.) (*Canis zerda*) 1.395 % (27.9 in 2000) (earlier statement 1.667 %: 25 in 1500);
Epomophorus gambianus (Ogilby) 1.401 % (4.33 in 309);
Rhinolophus ferrum-equinum (Schreb.) ♀ 1.489 % (0.350 in 23.5);
Hylobates lar leuciscus Geoffroy (*Hylobates leuciscus* Kuhl) ♀ 1.512 % (94.5 in 6250);
* *Sciurus vulgaris* L. ♀ 1.542 % (6 in 389);
Hylobates lar mulleri Martin (*Hylobates mulleri*) 1.585 % (86.1 in 5433);
Sciurus carolinensis Gm. 1.616 % (7.58 in 469);
* *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) ♂ 1.625 % (325 in 20000; body weight too light);
Nycticebus coucang (Bodd.) (*Nycticebus tardigradus* L.) ♂ 1.636 % (8.18 in 500);
Hylobates lar agilis F. Cuv. (*Hylobates agilis*) 1.659 % (93.3 in 5623);
* *Canis familiaris* L. "toy-terrier", "Zwergpinscher" 1.868 % (58.1 in 3110);
* *Sciurus vulgaris* L. 1.889 % (6.10 in 323);
Crocidura russula (Herm.) (*Sorex araneus* L.?) 1.932 % (0.17 in 8.8);
Mus musculus L. ♀ 2.048 % (0.43 in 21);
* *Homo sapiens* L. ♂ European average 2.092 % (1360 in 65000) (earlier statements 2.162 %: 1431 in 66200 and 2.182 %: 1375 in 63010 and 2.061 %: 1360 in 66000);
* *Homo sapiens* L. ♀ European average 2.259 % (1220 in 54000) (earlier statements 2.234 %: 1224 in 54800 and 2.367 %: 1235 in 52170);
Pippestrellus pipistrellus (Schreb.) (*Vesperugo pipistrella*) 2.308 % (0.150 in 6.5);
Tupaia javanica Horsf. ♂ 2.442 % (2.54 in 104);
Jaculus hirtipes (Licht.) (*Dipus hirtipes*) 2.534 % (1.85 in 73);
Sciurus hudsonicus (Erxl.) 2.579 % (4.1 in 159) (earlier statement 2.580 %: 4.103 in 159);
Eliomys quercinus (L.) 2.841 % (1.25 in 44);
Mustela nivalis L. (*Mustela vulgaris*) 3.000 % (1.95 in 65);
Callithrix jacchus (L.) (*Hapale jacchus*) 3.721 % (8 in 215) (earlier statement 3.724 %: 7.97 in 214);
Ateles geoffroyi Kuhl 3.820 % (95.5 in 2500);
Leontocebus rosalia (L.) (*Midas rosalia* L.) ♀ 3.821 % (12.8 in 335);
Sorex araneus L. (*Sorex vulgaris*) or *Sorex minutus* L. 4.310 % (0.125 in 2.9);
Saimiri sciureus (L.) (*Chrysothrix sciurea*) 6.000 % (24 in 400);
Cebus capucinus (L.) 9.615 % (125 in 1300).

So we see that as regards the relative quantity of brain *Homo* is inferior to a number of Mammalia with low body weights, of which Dubois (1897 *a*, p. 5; 1897 *b*, p. 339; 1897 *c*, pp. 2, 4; 1913, p. 593; 1914 *a*, p. 648; 1914 *b*, p. 328) mentions by name some small Monkeys and some of the smallest species of Insectivora and Chiroptera, though in the latter and in *Sorex* also the brains are at a very low degree of organisation. *Homo* is also surpassed in relative brain weight by a number of small Birds.

Dubois (1898, p. 441) mentions that in European women the relative weight of the brain is on an average 4–5 % lower than in men.

We are now able, on the score of the relative weights of the brain, to make a comparison between related animals of different sizes and the result we find (Dubois, 1913, pp. 593, 594; 1914 *a*, p. 648; 1914 *b*, p. 323; 1917, p. 288) is for instance, that according to the relative quantity of brain *Mus musculus* L. would be four times better provided with brain than *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus* = *Mus decumanus* Pallas), *Felis catus* L. (*Felis domestica* Gm.) five times better than *Panthera tigris* (L.) (*Felis tigris* L.) and *Panthera leo* (L.) (*Felis leo* L.), and the giant shrew (*Tupaia*??) would have three times less brain than the common shrew (*Sorex*??).

Comparing the relative size of the brain in the various classes of the Vertebrata it can be said that in the series of Amphibia, Reptilia, Aves and Mammalia the brain – and this holds good especially for the development of the telencephalon – is relatively larger in every later mentioned class than in the earlier mentioned one (Haller von Hallerstein, 1934, pp. 160, 167, 174). According to Dubois (1913, p. 597; 1914 *a*, p. 651; 1914 *b*, p. 328) the weight of the brain in the Pisces, Amphibia and Reptilia descends, both absolutely and relatively, as low as to the order of magnitude of about 10 % of that of the Aves and Mammalia. Cuvier already found that Pisces have proportionately less brain than Reptilia and Reptilia less than Mammalia; within every class, however, the relative weight of the brain leads to an impossible classification and therefore the relative weight of the brain is no suitable measure for relationship (Dubois, 1917, p. 288).

The relative weight of the brain provides important data for our insight in the size of the cavity for the brain, but as arrangement after the relative brain weights does not result in any rational classification even within each class, it does not offer us any general point of view.

We obtain a much more exact and more useful understanding by considering the weight of the brain as the product of two factors. One factor is a power of the body weight, namely the body weight raised to a power smaller than 1, the so-called exponent of relation. The other factor is a coefficient that expresses the relative cephalisation of the animal (Dubois,

1897 *a*, pp. 5, 27/28; 1897 *b*, pp. 339, 361/362; 1897 *c*, pp. 2, 18; 1913, p. 593; 1914 *a*, p. 647; 1914 *b*, p. 323; 1920 *a*, p. 83; 1922 *b*, p. 309; 1923, p. 232; 1924 *a*, p. 319; 1924 *b*, p. 430; 1928 *a*, p. 255; 1928 *b*, p. 308; 1930, pp. 248, 249; 1934 *a*, p. 185).

The connection between the weight of the brain and these two factors is expressed by the formula $E = k.P^r$, in which E = the weight of the encephalon, P = the weight of the body, k = the coefficient of cephalisation and r = the exponent of relation (Dubois, 1897 *a*, pp. 28/29, 32; 1897 *b*, pp. 363, 366; 1897 *c*, pp. 19, 21; 1913, p. 595; 1914 *a*, p. 649; 1914 *b*, pp. 324/325; 1917, p. 289; 1920 *b*, p. 623 foot note; 1920 *c*, p. 665 foot note; 1930, pp. 250/251; 1934 *b*, p. 74; 1938, p. 37).

In his publications of 1897 (1897 *a*, p. 30; 1897 *b*, p. 364; 1897 *c*, p. 20) and in those of 1913/1914 (1913, pp. 594/595; 1914 *a*, p. 649; 1914 *b*, p. 324) Dubois deduces the relation between the size of the brain and the size of the body from the relation between the quantity of brain and the extension of some receptive surface of sense.

In his later publications (see 1930, p. 260) the psychoencephalon is substituted for the whole brain in this product and in this formula. Dubois means by psychoencephalon the brain from the telencephalon up to and including the mesencephalon. Later on we shall deal with this subject again extensively.

This formula holds good only when the determination of the brain weight and the body weight comes up to Dubois' high standard with which we have become acquainted above. I may remind the reader of such requirements as full-grown adult animals, living in the free state of nature, where the weights in question represent the norm, *i.e.* where the animals are not too fat (domestic animals) nor too thin (specimens from zoological gardens, dead after disease); when other weights than these are used, an inaccurate result for the exponent of relation or the coefficient of cephalisation will be obtained (Dubois, 1897 *a*, p. 6; 1897 *b*, p. 340; 1897 *c*, p. 3; 1919 *a*, p. 516 foot note; 1919 *b*, p. 724 foot note; 1922 *b*, pp. 314, 316; 1923, pp. 237, 239; 1938, p. 38).

Dubois (1919 *a*, p. 503; 1919 *b*, p. 711) calls species of animals with the same coefficient of cephalisation homoneuric species; they are species with the same or equal organisation of the nervous system (see also 1920 *a*, p. 83; 1920 *b*, p. 623; 1920 *c*, p. 665; 1922 *c*, p. 317; 1924 *a*, p. 319; 1924 *b*, p. 430; 1930, p. 249). Homoneuric species generally belong to the same genera or families (Dubois, 1920 *a*, pp. 83, 85). In his earlier publications also Dubois (1897 *a*, pp. 4/5, 27, 28, 29/30; 1897 *b*, pp. 338, 361, 363, 364; 1897 *c*, pp. 2, 18, 19, 20; 1913, pp. 594, 600/601; 1914 *a*, pp. 648, 655; 1914 *b*, pp. 323/324, 334; 1917, pp. 289, 290; 1918 *a*, p. 1416; 1918 *b*, p. 1328) already defines homoneuric species of animals, without mentioning this term, as: animals with an equally high organisation of the brain, with brains of the same type, with an equal cephalisation of their central nervous system, accompanied by an equal morphological and physiological organisation, an equally high organisation of the body and an equal shape of their bodies; such species of animals are near to one another, systematically and in their manner of life.

So homoneuric species of animals have one and the same cephalisation. Dubois means by cephalisation (1897 *a*, pp. 5,19, 27; 1897 *b*, pp. 339, 353, 362; 1897 *c*, pp. 2, 12, 18; 1913 *a*, p. 593; 1914 *a*, p. 647; 1914 *b*, p. 323; 1922 *b*, p. 309; 1923, p. 232; 1924 *a*, p. 319; 1924 *b*, p.430; 1928 *a*, p. 255; 1928 *b*, p. 308; 1930, pp. 248, 289; 1934 *a*, p. 185) the complexity of the brain, the stage of development attained by the brain, the degree of the organisation of the brain. Thus equal cephalisation means equal quantity of the brain in function of the body weight (Dubois, 1919 *a*, p. 519; 1919 *b*, p. 727). Dubois (1920 *a*, p. 82; 1930, p. 249) defines the cephalisation as the relative development of the size of the brain, as the relative quantity of that part of the nervous system which is enclosed in the skull. The coefficient of cephalisation denotes higher or lower number of nervous centra characteristic for the species, the genus or the family (Dubois, 1938, p. 37). According to Dubois (1922 *b*, pp. 309/310; 1923, pp. 232/233) the cephalisation of the central nervous system is determined by the stage of development of the brain, by the particular structure and functions of other organs and by other not easily measurable factors.

Passing on to a discussion of the value of the various factors in the formula given above, a separate discussion is desirable of the differences between both sexes of one and the same species of animals, between the various individuals of one and the same sex within a single species of animal (varieties, races), between homoneuric species of animals and between heteroneuric species of animals (species of animals with a different coefficient of cephalisation); the differences within one single family, one single order, but also those between the classes of the Vertebrata will be discussed in this connection.

In both sexes

Assuming in our comparison of the two sexes of one and the same animal species that the coefficient of cephalisation is the same in both sexes, then the factor k is eliminated from the proportion $E : e = k.P^R : k.p^r$ and we can calculate the relation of both exponents of relation. Dubois (1919 *c*, p. 713; 1919 *d*, p. 850) calls it the intersexual exponent of relation.

For *Homo sapiens* L. this intersexual exponent of relation amounts to 0.56 (Dubois, 1917, p. 290; 1918 *a*, p. 1416; 1918 *b*, p. 1328; 1919 *c*, pp. 714, 726; 1919 *d*, pp. 851, 863). Now in *Homo* the intersexual exponent of relation is equal to that between homoneuric animal species of different size and weight (Dubois, 1913, p. 604; 1914 *a*, p. 658; 1914 *b*, p. 337; 1919 *c*, pp. 714, 715; 1919 *d*, pp. 851, 852). All this holds good, if one assumes the coefficient of cephalisation of man and woman to be equal; if one does not do so, the result will be, as we shall see later on, that 2/9 defines the relation of cephalisation between man and woman and apparently not the interspecific exponent 5 9 (Dubois, 1938, p. 46). So in woman the size of the brain is smaller than in man, calculated for the same body weight; the cranial capacity of woman is 6 % lower than in man; this is a typical secondary sexual difference (Dubois, 1934 *a*, p. 186). Within each of the sexes the brain weight again varies in connection with the body size, as will be discussed later on. In this respect man and woman behave as two distinct series, like two species, showing a discontinuity from one sex to the other (Dubois, 1919 *c*, p. 714; 1919 *d*, p. 851). Concerning man and woman we have many data at our disposal, which makes the determination of averages possible, but for the rest we have few data (Dubois, 1919 *c*, p. 714; 1919 *d*, pp. 850/851).

For the Monkeys Dubois (1913, p. 605; 1914 *a*, pp. 658/659; 1914 *b*, p. 338; 1919 *c*, pp. 718, 719, 720; 1919 *d*, pp. 855, 856, 857) gives calculations for the intersexual exponent of relation of *Trachypithecus pyrrhus* (Horsf.) (*Presbytes* (*Semnopithecus*) *maurus* F. Cuv.), which also amounts to about 0.56 and therefore is equal to that of *Homo*. According to Dubois (1919 *c*, pp. 718, 721; 1919 *d*, pp. 855, 858) we find this sexual dimorphism of the brain weight certainly in many if not in all the Monkeys, at least in those of the Old World, for they show universally considerable sexual differences in size of the body and at the same time a certain sexual difference in the requirements of the mode of life.

This sexual dimorphism of the brain weight does not hold good for the Vertebrata in general (Dubois, 1913, p. 605; 1914 *a*, pp. 658/659; 1914 *b*, p. 338; 1919 *c*, p. 715 foot note; 1919 *d*, p. 852 foot note). Dubois (1919 *c*, pp. 715, 716, 717, 718, 721, 726; 1919 *d*, pp. 852, 853, 854, 855, 858, 863) calculated the intersexual exponent of relation for *Passer domesticus* L., *Colinus virginianus* (L.), *Gallus gallus* (L.) dom., *Canis familiaris* L., *Felis catus* L. (*Felis domestica* Gm.), *Bos taurus* L. and *Ovis aries* L. and sometimes found no difference between the sexes or such a low exponent of relation, that it is very nearly 0.28, the interindividual exponent for equal sexes, so that the discontinuity in the transition from the one sex to the other, which is so striking in the human species, does not exist. Probably for by far the most animal species there does not exist sexual dimorphism in the brain weight, whether or not they are externally sexually dimorphous. Even for animals as *Bos taurus* L. and *Gallus gallus* (L.) dom., which show such a large sexual dimorphism in the size of their bodies, cerebral dimorphism is lacking, probably even for Pinnipedia, though of some species of this order the males are on an average three or four times heavier than the females. This phenomenon, the fact namely, that externally dimorphous animal species do not always show the same intersexual exponent of relation as homoneuric animal species, means for Dubois (1919 *c*, pp. 714/715, 720; 1919 *d*, pp. 851/852, 857) that the high intersexual exponent of relation in *Homo* and in Monkeys cannot be a question of the size of the body alone, but that yet another difference is involved and that a qualitative difference, in contrast also with two homoneuric species, the body weights of which are only different as far as the quantity is concerned. According to Dubois (1919 *c*, pp. 721, 725/726, 727, 729, 730; 1919 *d*, pp. 858, 863, 864, 866/867) the cause of the sexual dimorphism of the brain weight in Man lies in the disproportionally slighter muscularity of the human female. This also occurs in *Pongo pygmaeus* (Hopp.) (*Simia satyrus* auct.) (Dubois, 1921, pp. 1003/1004; 1922 *a*, p. 1287).

In various individuals of the same species

When comparing the weight of the brain in relation to the weight of the body of various individuals of the same sex within one single animal species, we may have to do with differences, due to different states of nutrition of the individuals (fat, thin), with differences connected with the variability of the adult normal individual and finally with differences due to racial differences.

In the above we have already pointed out the influence of a too fat or an emaciated condition of the individual on the weight of the body and on that of the brain; proportionately the influence on the latter is much slighter than on the weight of the body, as we have already seen. Furthermore we noted that Dubois tries to avoid these very figures and to use only data obtained from adult, full-grown, normal individuals.

The differences between adult, normal individuals of one and the same sex within a certain animal species, which can be accounted for by the variability of that species, can be expressed in the magnitude of the exponent in the formula $E = k.P^R$. The exponent holding between the adult individuals of one and the same species, in relation of the body weight to the brain weight, may be called the ontogenetic exponent, as it expresses the relative individual growth of the brain to the adult state according to Dubois (1922 *b*, pp. 318, 324; 1923, pp. 240/241, 247; 1930, p. 250; 1934 *a*, p. 185). It is also called interindividual exponent or factor of correlation (Dubois, 1913, p. 603; 1914 *a*, p. 657; 1914 *b*, p. 336; 1919 *c*, pp. 713, 717; 1919 *d*, pp. 850, 854; 1922 *b*, p. 313; 1922 *c*, p. 318; 1923, p. 236).

For such comparisons of the individuals only few species, such as *Canis familiaris* L. and also *Equus caballus* L. on one side and Man on the other side, are suitable (Dubois, 1913, p. 601; 1914 *a*, p. 655; 1914 *b*, p. 334; 1919 *c*, p. 713; 1919 *d*, p. 850; 1922 *b*, p. 313; 1922 *c*, p. 318; 1923, p. 236; 1930, p. 250). *Canis familiaris* L. and also *Equus caballus* L. show very important differences of the body weights, Man less, but Man is most suitable by the numerousness of the observations of weight.

For Man, at any rate for the European, Dubois (1898, pp. 430/431, 433, 438; 1913, pp. 601, 604; 1914 *a*, pp. 655, 658; 1914 *b*, pp. 334/335, 337; 1917, p. 290; 1919 *c*, p. 726; 1919 *d*, p. 863; 1922 *b*, pp. 312/313; 1923, pp. 235/236) states as value of the ontogenetic exponent within each of the two sexes successively: round 0.25, the value of 0.245 being probably more correct; the principle ("prinzipielle") exponent of correlation would be 0.22, the real one being somewhat higher; then again 0.28 and finally about 0.25 and in the neighbourhood of 0.27 or lower. For the Australian aboriginals DUBOIS (1922 *b*, pp. 314/315; 1923, p. 237) states a value of 0.2770. In his last papers DUBOIS (1928 *a*, p. 255; 1928 *b*, p. 308; 1930, p. 253; 1934 *a*, p. 185) states that the ontogenetic exponent between full-grown individuals of the same sex amounts to 0.24 in *Homo sapiens* L., in the European at any rate, the same as in other domesticated animal species or races, thus somewhat smaller than 0.28 or 5/18 (the value of the ontogenetic exponent in species living in the natural state).

For *Canis familiaris* L. DUBOIS (1913, pp. 602/603/604; 1914 *a*, pp. 656/657 658; 1914 *b*, pp. 335/336/337; 1922 *b*, pp. 312/313; 1923, pp. 235/236) states at first 0.25 and about 0.25, *i.e.* less than 5/18, later DUBOIS (1922 *c*, pp. 317/318; 1930, p. 253 foot note; 1934 *a*, p. 185) states as value 0.24. For the value of this factor in this animal as a domesticated animal I refer to DUBOIS' remarks placed above at the end of the paragraph on the value of this ontogenetic exponent in Man.

Also for a number of other animals DUBOIS (1913, pp. 603/604; 1914 *a*, pp. 657/658; 1914 *b*, pp. 336/337; 1922 *b*, pp. 313/314, 316; 1923, pp. 236/237, 239) has determined, calculated or copied the ontogenetic exponent, as for *Sciurus carolinensis* Gm. (0.20; 0.338), *Talpa europaea* L. (0.234), *Equus caballus* L. (0.2708; 0.2528; 0.1855), *Oryctolagus cuniculus* (L.) (*Lepus cuniculus*) (0.2512), *Anas platyrhyncha* L. dom. (0.3096), *Gallus gallus* (L.) dom. (0.2248), wild *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus*) (0.1674; 0.1572; 0.1554), domesticated albino *Rattus norvegicus* (Berkenhout) (0.1342) and *Rana catesbeiana* Shaw (0.2516; 0.2310; 0.2316). For this and other reasons DUBOIS is of the opinion that the ontogenetic exponent of relation is one and the same for all Vertebrata. At first (DUBOIS, 1913, pp. 603, 604; 1914 *a*, pp. 657, 658; 1914 *b*, pp. 336, 337; 1917, p. 290; 1918 *a*, pp. 1416, 1424; 1918 *b*, pp. 1328, 1336) it was fixed at 0.22, first with the addition that it is the fundamental exponent of relation, the real one being a little higher. Afterwards DUBOIS states (1919 *c*, pp. 713, 726; 1919 *d*, pp. 850, 863) that with the available data it could not be ascertained whether the ontogenetic exponent is 0.22 or 0.25 or 0.28, but DUBOIS continues, that he becomes more and more inclined to consider 0.28, more accurately 0.277 . . ., as the correct interindividual factor. That is why DUBOIS (1922 *b*, pp. 313, 324; 1923, pp. 236, 247; 1922 *c*, p. 318; 1928 *a*, p. 255; 1928 *b*, p. 308; 1930, p. 253 foot note) in his subsequent papers fixes this exponent at 0.28 or 5/18, sometimes at 0.27 or lower. Only in one of his last publications this exponent is fixed at about 2/9 by DUBOIS (1938, p. 38).

The domesticated animals and *Putorius putorius* (L.) form an exception to this value of the ontogenetic exponent. In *Putorius putorius* (L.) the ontogenetic exponent is 0.42 according to DUBOIS (1922 *b*, p. 326; 1923, p. 249); this exponent is exactly halfway between 5/18 and 5/9. Evidently the species *Putorius putorius* (L.) is in a state of desintegration, probably the other *Putorius* species are too.

In the above we saw already that according to DUBOIS (1928 *a*, p. 255; 1928 *b*, p. 308; 1930, p. 253; 1934 *a*, p. 185) the ontogenetic exponent is lower than 0.28 namely 0.24 in domesticated animal species or races. As a consequence of domestication the brain weight has been reduced and in the cases that the body weight too has been reduced, as, *e.g.*, in *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus*), the brain weight has been reduced to a comparatively greater degree, due to a diminished growth of the brain; the result is a lower value of the exponent in domesticated species or races (DUBOIS, 1922 *b*, pp. 315–317; 1923, pp. 238–240). In *Canis familiaris* L. the brain weight is certainly at least 6 %, probably 10 % lower than in a wild species of *Canis* of the same weight (DUBOIS, 1922 *b*, p. 315; 1923, p. 238). So also in Dogs the domesticated animal with its higher "civilisation" yet has a smaller quantity of brain (DUBOIS, 1922 *c*, p. 315). In the domesticated *Oryctolagus cuniculus* (L.) too the size of the brain according to NACHTSHEIM (BÖKER, 1937, p. 193) has changed in comparison with the wild *Oryctolagus cuniculus* (L.).

According to DUBOIS (1918 *a*, pp. 1422, 1424; 1918 *b*, pp. 1334, 1336; 1919 *c*, p. 713; 1919 *d*, p. 850; 1922 *b*, pp. 317, 321, 324/325, 326; 1923, pp. 240, 243/244, 247/248, 249; 1922 *c*, p. 318) a possible explanation of the value of this ontogenetic or interindividual exponent may be found in the increasing volume of the nerve cells.

In different races

Apparently in the inquiry into the ontogenetic exponent discussed in the above, racial differences were not taken into account. In Dogs, for instance, divergent classes of body weight are distinguished, but the material is not classified as to races. Dubois (1934 *a*, pp. 189–193) mentions the racial differences only concerning Man and, for want of sufficient data on brain weight, he deals with the differences between the cranial capacities *i.e.* the size of the cranial cavity for the brain. Thus in the Australian the cranial capacities are rather low, in the Eskimo rather high as also in † *Homo neanderthalensis* King. These differences are explained by Dubois from differences in body weight and in muscular development. Finally Dubois (1928 *a*, p. 254; 1928 *b*, p. 307) quotes two "rules" by O. C. Marsh, where races are discussed, namely: "The brain of a mammal belonging to a vigourous race, fitted for a long survival, is larger than the average brain, of that period, in the same group" and "The brain of a mammal of a declining race is smaller than the average of its contemporaries of the same group". To all probability it is not a matter of racial differences here, but of differences in species.

As the value of the interindividual or ontogenetic exponent is low, the differences between the sizes of the cranial cavities for the brain are not conspicuous either, though certainly they will have to be taken into account upon an accurate investigation.

Much more conspicuous is the difference in size of the brain and also of the cranial cavity for the brain between domesticated individuals of various sizes and wild species of corresponding sizes. According to Dubois (1922 *b*, pp. 318/319; 1923, p. 241) in consequence of the difference in the fixed relations of the weights of the brain and the body, between homoneuric species on one side, individuals of a species on the other side, *i.e.*, the difference between the phylogenetic and the ontogenetic exponent, small individuals have comparatively more, large individuals comparatively less brain than species of corresponding mean body weight. The amount and the plus or minus sense of this difference with wild species is dependent on their body weight. The smaller the wild species of the genus *Canis*, the more it is exceeded in brain weight by an individual of the same size (the same body weight) of *Canis familiaris* L. The brain weight in the diminutive individual of *Canis familiaris* L., with only a ninth of the mean body weight of the species (18000 grams), thus a toy-terrier, a "Zwergpinscher" (of 2000 grams), is quite 87 % more than the mean of *Fennecus zerda* (Zimm.)

(*Canis zerda*), the smallest species of Canidae. Domestic Dogs of the size (the body weight) of *Vulpes vulpes* (L.) have only 28.4 % more brain weight than this Fox. The difference of *Thos aureus* (L.) (*Canis aureus*) from Dogs of the body weight of this species is 20.1 % (*Thos aureus* (L.) has a higher cephalisation!). In contrast with domestic Dogs of the size of these small Canidae, very large domestic Dogs, of about 40000 grams, *i.e.*, the mean body weight of *Canis lupus* L., have 24.8 % less brain weight than *Canis lupus* L. (Dubois, 1922 *b*, pp. 319, 320; 1923, pp. 241/242, 243; 1922 *c*, pp. 316/317; 1930, p. 254). We may add, that an adult *Canis familiaris* L. of the size of *Canis lupus* L., thus of about 40000 grams body weight, has double the brain weight of a lap-dog, weighing about 2000 grams (Dubois, 1922 *b*, p. 309; 1923, p. 232).

In homoneuric species of animals

We shall now pass on to a discussion of the relation between the brain weight and the body weight in homoneuric animal species, that is to say animal species having reached the same height of cephalisation, as we already saw above. *Felis catus* L. (*Felis domestica* Gm.) and *Panthera tigris* (L.) (*Felis tigris* L.), *Mus musculus* L. and *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus*), *Cephalophus* (*Guevei*) *maxwellii* (Ham. Sm.) and *Oryx beisa* (Rüpp.) are examples of homoneuric animal species; indeed, all Felidae, all Canidae, all Bovidae the Cervidae added, all Leporidae, all Muridae each in themselves are homoneuric groups (Dubois, 1922 *b*, p. 310; 1923, p. 233; 1930, pp. 252/253).

Among homoneuric animal species the species with the highest body weight always have the absolutely heaviest brain (Dubois, 1897 *a*, pp. 4/5; 1897 *b*, p. 338; 1897 *c*, p. 2; 1920 *a*, p. 83; 1930, p. 249). The relation, however, between brain weight and body weight is not proportional. The smaller species have relatively higher weights of the brain, or in other words, as the size of the body increases, the weight of the brain increases to a less extent than the body weight, a phenomenon to be observed in all Vertebrata and already known to Cuvier and Marsh (Dubois, 1897 *a*, pp. 5, 6, 23; 1897 *b*, pp. 339, 340, 357; 1897 *c*, pp. 2, 3, 15; 1913, p. 594; 1914 *a*, p. 648; 1914 *b*, pp. 323, 324; 1917, p. 288; 1918 *a*, p. 1424; 1918 *b*, p. 1336; 1920 *a*, pp. 83/84; 1922 *b*, p. 310; 1923, p. 233; 1928 *a*, p. 254; 1928 *b*, pp. 307/308; 1930, p. 249). Dubois (1922 *b*, p. 310; 1923, p. 233) adds as a general illustration that the large species of the genus *Canis*, and also the large adult individual of the Domestic Dog species always has less brain weight in ratio to the body weight than the small species and the small adult individual.

Others have stated the case as follows: in the first place, the brain does not increase in ratio to the weight of the body and secondly, the relative brain weight as a rule - to which, however, exceptions are found – diminishes when the body weight increases, within a natural group; consequently within such groups small animals have a relatively large brain and large animals a relatively small brain (HALLER VON HALLERSTEIN, 1934, pp. 23/24; MARINELLI, 1936, p. 811). The relation between the size of the brain and of the body may also be expressed in this way, that – and this is especially clear in Aves and Mammalia – the size of the brain is so to say tied down to a certain magnitude in that sense, that the brain cannot decrease below a certain (high) minimum of magnitude, so that in a sense the size of the brain is more absolute than relative (STADTMÜLLER, 1936, p. 951).

To determine the accurate relation between the weight of the brain and that of the body DUBOIS (1920 *a*, p. 85; 1928 *a*, p. 255; 1928 *b*, pp. 308/309) says we shall have to find the law, expressing the relation between brain weight and body weight in such a way, that we get not only equal values of the relative cephalisation k in homoneuric animal species, but also with heteroneuric animal species values for k corresponding with our conceptions of the powers of the brain and of the grouping of the species in the natural system, thus a sequence of the Mammalia which – leaving aside certain exceptions to the rule – is nowhere in contradiction to the natural system, if the k is calculated for the psychoencephalon. The formulation of this law, namely in the form $E = k.p^R$, has already been mentioned before. DUBOIS calls the factor R the exponent of relation, as we have seen. Later on he calls this factor also the phylogenetic exponent, as this exponent indicates the relation of species to species, a relation which must have come about with the origination of the species (DUBOIS, 1922 *b*, pp. 311, 324; 1923, pp. 234, 247; 1928 *a*, p. 255; 1928 *b*, p. 308; 1930, p. 250).

Already in his earliest papers on this subject DUBOIS (1897 *a*, pp. 28, 29/30; 1897 *b*, pp. 362, 363/364; 1897 *c*, pp. 18, 19/20) argued that on account of the influence of the difference in development of the surface of the sensory organs this exponent of relation practically always had to be smaller than 0.66 . . . Forthwith an average of 0.56 for this value was stated by Dubois (1897 *a*, p. 31; 1897 *b*, p. 366; 1897 *c*, p. 21; 1898, pp. 423, 433; 1917, pp. 289, 290). Soon afterwards he determined the value more accurately on 5/9 or 0.55 . . . (Dubois, 1913, pp. 595/596, 600/601; 1914 *a*, pp. 649/650, 655; 1914 *b*, pp. 325, 334; 1919 *c*, p. 713; 1919 *d*, p. 850; 1920 *b*, pp. 623, 634; 1920 *c*, pp. 665, 676; 1930, p. 251). Not only does this factor apply to the Mammalia, but to all classes of Vertebrata (Dubois, 1913, pp. 596, 598, 600, 600/601; 1914 *a*, pp. 650, 652, 654, 655; 1914 *b*, pp. 328, 331, 333, 334; 1917, pp. 289, 290; 1920 *a*, pp. 85/86; 1922 *b*, pp. 310/311; 1923, pp. 233/234; 1924 *a*, p. 319; 1924 *b*, p. 430; 1930, p. 251; 1934 *b*, p. 74; 1938, pp. 38, 39).

The few data known for the Amphibia yield a lower exponent of relation; Dubois, however, has no doubt that for Amphibia too this exponent is 0.55 . . . (Dubois, 1913, pp. 598/599; 1914 *a*, pp. 652/653; 1914 *b*, pp. 331/332; 1917, p. 290; 1920 *a*, p. 86; 1930, p. 251; 1938, p. 38).

Now the fact presents itself, that in a number of cases the exponent of relation is not 0.55 . . ., but 0.66, *e.g.*, in *Anguilla anguilla* (L.). This phenomenon should be ascribed to the reduction of the eye. That is why in the Ophidia, where the eyes are well developed, the exponent of relation is 0.56 (Dubois, 1917, p. 291). Much more detailed is Dubois' discussion of the Chiroptera (1897 *a*, pp. 32/33; 1897 *b*, pp. 366–368; 1897 *c*, pp. 21/22; 1913, p. 611; 1914 *a*, p. 666; 1914 *b*, pp. 325, 327, 347; 1917, p. 291; 1938, pp. 38, 39), where both in the Microchiroptera and in the Megachiroptera, including the Phyllostomidae, the exponent of relation is also 0.66. In the Chiroptera too the eye is reduced and the sense of touch in the skin is strongly developed, and the sense of hearing as well. In the Chiroptera the exponent 0.66 is found, when the weight of the whole brain is brought into account. When the weight of the psychoencephalon only is taken, the Chiroptera are also found to have the exponent 0.55 . . . (Dubois, 1928 *a*, p. 256; 1928 *b*, p. 309; 1938, p. 38). Later on we shall revert to the deviating relation of the psychoencephalon to the whole of the brain.

From the general validity of the value 5/9 or 0.55 . . . for the exponent of relation Dubois (1914 *b*, p. 339; 1920 *a*, p. 86; 1922 *b*, p. 311; 1923, p. 234) conludes that this is a rational law and not an empirical law.

Already in his first papers Dubois (1897 *a*, pp. 23, 26/27, 32; 1897 *b*, pp. 357, 361/362, 366; 1897 *c*, pp. 15, 17/18, 21) looks for an explanation of the value 0.55 . . . or rather of its deviation from 0.66 . . . which latter figure would express proportionality to the surface of the body; he ascribed it to the metabolic processes (influenced by the size of the surface of the sensory organs and the magnitude of muscular labour) combined with influence of the thickness of the cerebral cortex. Later on Dubois has abandoned this explanation (1930, p. 252). – Between homoneuric species, under for the rest equal circumstances, the weight of the brain varies proportionally to $M^{0.56}$ and $P^{0.56}$ in which $M =$ muscle weight and $P =$ body weight (Dubois' 1919 *c*, p. 729; 1919 *d*, pp. 866/867). In later publications (1917, p. 290; 1920 *a*, pp. 86/87; 1930, pp. 249, 250) Dubois points out that the receptive surfaces of the sensory organs are out of proportion to the surface of the body, this especially applies to the eye. This, finally, is explained by Dubois (1919 *a*, p. 503; 1919 *b*, p. 711; 1920 *a*, p. 87; 1920 *b*, pp. 623, 634; 1920 *c*, pp. 665, 676; 1922 *b*, pp. 321, 324, 325; 1923, pp. 243/244, 247, 248; 1922 *c*, p. 318; 1924 *a*, p. 319; 1924 *b*, p. 430; 1930, pp. 253, 279) as follows: the volume of each nerve cell and the number of nerve cells in homoneuric animal species increases in the same ratio, so that the result will be that on the ground of both factors nerve cells increase proportionally to $P^{0.55}$, so in the same way as the brain.

In homoneuric animal species – contrary to heteroneuric animal species – gradual transition is possible (Dubois, 1928 *a*, pp. 258/259; 1928 *b*, pp. 313/314). In each stage of cephalisation we find the forms grow to very different sizes. Moreover they diverge greatly in form and function by specialisation, as, *e.g.*, *Talpa*, *Desmana* with *Galemys* (*Myogale*), *Erinaceus* and *Potamogale* (Dubois, 1928 *b*, p. 312).

Very important for our purpose – the relations of the size of the cranial cavities for the brain – are the few examples that Dubois gives of the relation of the relative weights of the brain and the numerous examples of the relation of the absolute weights of the brain in homoneuric animal species.

Dubois mentions the following examples of the relation of the relative brain weights (1897 *a*, p. 5; 1897 *b*, p. 339; 1897 *c*, p. 2): *Felis catus* L. (*Felis domestica* Gm.) 0.943 % (read in my opinion 0.939 %) compared with *Panthera leo* (L.) (*Felis leo* L.) 0.183 %;

Mus musculus L. 2.041 % (read in my opinion 2.048 %) compared with *Rattus norvegicus* (Berkenhout) (*Mus decumanus* Pallas) 0.526 % (read in my opinion 0.527 %); *Sciurus vulgaris* L. 1.538 % (read in my opinion 1.542 %) compared with *Ratufa bicolor* (Sparrm.) (*Sciurus bicolor* Sparrm.) (of the size of a Rabbit) 0.862 % (read in my opinion 0.857 %) and *Cephalophus* (*Guevei*) *maxwellii* (Ham. Sm.) 1.136 % (read in my opinion 1.132 %) compared with *Oryx beisa* (Rüpp.) 0.262 %.

Of the relation of the absolute brain weights in homoneuric animal species Dubois gives the following examples.

A medium-sized *Perca fluviatilis* L., weighing 37 times as much as a *Gasterosteus aculeatus* L., has eight times its brain weight; a *Varanus* having 446 times the body weight of a *Lacerta viridis* (Laur.), has 26 times its brain weight; *Aquila chrysaëtos* (L.), having 23 times the body weight of *Falco tinnunculus* L., has 5 times its brain weight (Dubois, 1920 *a*, p. 84).

In the very homomorphous family of the Felidae, which differ so greatly in body size and weight, the body weight is varying in the ratio 1 to 100 (Dubois, 1928 *a*, p. 255; 1928 *b*, pp. 309, 311/312; 1930, pp. 252/253). *Panthera leo* (L.) (*Felis leo* L.), whose body weight is 36 times as large as that of *Felis catus* L. (*Felis domestica* Gm.), has an absolute weight of the brain 7 times larger or 7 times as large as that of *Felis catus* L. (Dubois, 1897 *a*, pp. 4/5; 1897 *b*, p. 338; 1897 *c*, p. 2; 1898, p. 423; 1913, p. 594; 1914 *a*, p. 648; 1914 *b*, p. 324; 1920 *a*, p. 84). *Panthera tigris* (L.)(*Felis tigris* L.) with 64 times or 55 times or 50 times the body weight of *Felis catus* L. possesses 10 × or 9 × its brain weight (Dubois, 1922 *b*, p. 309; 1923, p. 232; 1924 *a*, p. 319; 1924 *b*, p. 430; 1930, p. 249). *Puma concolor* (L.) (*Felis concolor*), 13 times heavier than *Felis catus* L., has 4½ times its brain weight (Dubois, 1920 *a*, p. 84). *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus* = *Mus decumanus* Pallas), being 21 times or 17 times as heavy as *Mus musculus* L., has a brain weight 5½ times larger or as large or 6 times as much brain (Dubois, 1897 *a*, pp. 4/5; 1897 *b*, p. 338; 1897 *c*, p. 2; 1898, p. 423; 1913, p. 594; 1914 *a*, p. 648; 1914 *b*, p. 324; 1924 *a*, p. 319; 1924 *b*, p. 430). *Oryx beisa* (Rüpp.), which has the body size of the European deer, *Cervus elaphus* L., has a brain rather more than 7 times as heavy as *Cephalophus* (*Guevei*) *maxwellii* (Ham. Sm.), which has the body size of a *Lepus europaeus* Pall. (Dubois, 1897 *a*, pp. 4/5; 1897 *b*, p. 338; 1897 *c*, p. 2). The brain of *Elephas* weighs 10 times as much as that of *Bos taurus* L., but the body weight too is about 10 times as much (DUBOIS, 1897 *a*, p. 40; 1897 *b*, pp. 374/375; 1897 *c*, p. 26).

In heteroneuric species of animals (cephalisation)

Let us now pass on to what DUBOIS tells us about cephalisation. Already in the above we saw what he understands by this term.

We may form an idea of cephalisation when comparing various species of animals of the same body weight and of the same body size (DUBOIS, 1897 *a*, p. 19; 1897 *b*, p. 353; 1897 *c*, p. 12; 1922 *b*, p. 310; 1923, p. 233). DUBOIS gives the following examples. A large parrot whose body weight is equal to that of *Anas querquedula* L. has $2\frac{1}{2}$ times as much brain (DUBOIS, 1920 *a*, p. 83).

Concerning the Mammalia DUBOIS (1897 *a*, p. 4; 1897 *b*, p. 338; 1897 *c*, pp. 1/2) states that not a single animal or mammal of the same body size as Man has such a large quantity of brain as Man. The large Anthropoid Apes whose body weight is about equal to that of Man do not even reach $^1/_3$, Dogs of the same weight only reach $^1/_{10}$ of the weight of the brain of Man. Man possesses three times the brain weight of a species of Anthropoid Apes of the same body weight and more than six times the brain weight of an equally heavy *Gazella* sp. The coefficient of cephalisation of Man is three times as great as that of Anthropoid Apes and more than six times as great as that of the *Gazella* sp. (DUBOIS, 1922 *b*, p. 310; 1923, p. 233). *Leontocebus rosalia* (L.) (*Midas rosalia* L.) with 1 gram brain weight per 26 gram body weight, has about the same body weight as *Sciurus vulgaris* L., which has 1 gram of brain per 65 gram body weight and so the former has double the weight of the brain of the latter species (DUBOIS, 1897 *a*, p. 4; 1897 *b*, p. 338; 1897 *c*, p. 2; 1920 *a*, p. 83). *Homo sapiens* L. has $3\frac{1}{2}$ times the brain weight of a *Pan troglodytes* (Blumenbach) with equal body weight; *Pan troglodytes* (Blumenbach) has twice as much brain as would possess a *Macacus*, obtaining the same body weight and ten times as much brain as a Mouse or a Rat of the same body weight (DUBOIS, 1920 *a*, p. 83; 1920 *b*, pp. 624/625; 1920 *c*, p. 667). Of two animals of equal body size, but of a very different degree of organisation, the higher animal always has the heaviest brain. DUBOIS (1897 *a*, p. 4; 1897 *b*, p. 338; 1897 *c*, p. 2) illustrates this by the following examples: *Hylobates* (*Symphalangus*) *syndactylus* (Desm.) (brain weight 1.37 % of the body weight), *Trachypithecus pyrrhus* (Horsf.) (*Semnopithecus maurus* F. Cuv.) (idem 0.794 %), *Civettictis civetta* (Schreb.) (*Vi-*

verra civetta Schreb.) (idem 0.495 %) and *Manis javanica* Desm. (idem 0.163 %). *Equus caballus* L. having an average body weight 6 times as heavy as *Homo sapiens* L., possesses less than half its average brain weight (Dubois, 1897 *a*, p. 4; 1897 *b*, p. 338; 1897 *c*, p. 2).

The factor or coefficient of cephalisation can be calculated from the formula $E = k.p^R$, as was shown before (Dubois, 1897 *a*, pp. 33–35; 1897 *b*, pp. 368–370; 1897 *c*, pp. 22/23; 1928 *a*, p. 255; 1928 *b*, p. 308; 1934 *b*, p. 74; 1938, p. 39). If we take $R = 5/9$, then we get equal values of k for animal species which are considered as similar in their whole organisation, as *Panthera tigris* (L.) (*Felis tigris*) and *Felis catus* L. (*Felis domestica*), *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus*) and *Mus musculus* L.; if we take an other value for R, the fact presents itself that we get rather divergent values for k (Dubois, 1928 *a*, p. 255; 1928 *b*, pp. 308/309; 1930, p. 252). Earlier in this paper we already pointed out Dubois' requirements for the determination of the weights of the brain and of the body, which have to be taken from normal, full-grown specimens *etc. etc.*; in the same way this is of great importance for the calculation of the coefficient of cephalisation (Dubois, 1897 *a*, p. 41; 1897 *b*, pp. 338 foot note, 375/376; 1897 *c*, pp. 2 foot note, 27; 1928 *a*, p. 255; 1928 *b*, p. 308).

The coefficient of cephalisation expresses the relative cephalisation of the animal in question, that is the quantity of brain per unit of the surface of the body; so the figure has a relative meaning only, denoting the relative quantities of brain in the animals compared (Dubois, 1897 *a*, p. 27; 1897 *b*, p. 362; 1897 *c*, p. 18; 1938, p. 39).

Already in his first papers Dubois (1897 *a*, p. 34; 1897 *b*, p. 369; 1897 *c*, p. 23) says, that it would perhaps be better to take into account the hemispherae cerebri only and not the entire brain for the determination of the coefficient of cephalisation. Until his publication of 1928 Dubois determined the coefficient of cephalisation of the whole brain, after that, however, the psychoencephalic coefficient of cephalisation. Dubois (1928 *a*, p. 256; 1928 *b*, p. 309; 1930, pp. 254, 256, 257; 1928, p. 37) states that the Lower Tertiary Mammalia taught us, that strictly the psychoencephalon alone should have been taken into consideration; the same applies to the recent Insectivora and Microchiroptera, which are on the lowest level of cephalisation; in all these groups mentioned the psychoencephalon has a much smaller relative share of the total volume of the encephalon. Among the living mammalian species there are some in which the volume of the cerebellum has considerably increased secondarily and independently, namely doubled. In all these cases the cephalisation of the psychoencephalon must be taken into consideration in itself. For the rest the following holds good for Mammalia: the ratio of volume and weight of the psychoencephalon to the other parts of the brain, which moreover in most cases have a subordinate volume and weight, differ little. Hence the relations of the quantity found for the encephalon to those of the body can in general be considered as also valid for the psychoencephalon. MARSH already argued that in the oldest placental Mammals of all the parts of the brain especially the hemisphaerae cerebri were only very little developed (DUBOIS, 1897 *a*, pp. 3/4; 1897 *b*, p. 337; 1897 *c*, p. 1).

By psychoencephalon DUBOIS (1928 *a*, p. 253; 1928 *b*, pp. 305, 306; 1930, p. 254 foot note; 1938, pp. 37/38) understands that part of the encephalon which in morphology is called the prosencephalon. Besides the hemisphaerae cerebri also the rhinencephalon, thalamencephalon and mesencephalon belong to the psychoencephalon. According to its functions it is the direct and most highly specialised organ of the psychic functions. There exists, however, no special part of the brain or quantity of brain that is clearly destined for psychic functions only (DUBOIS, 1920 *a*, p. 84; 1920 *b*, p. 625; 1920 *c*, p. 667).

For our purpose – an insight into the size of the cerebral capsule to be obtained here from our knowledge of the size of the brain – the psychoencephalic coefficient of cephalisation, where it deviates from the coefficient of cephalisation of the whole brain, is of little value. For then we should have to calculate the size of the psychoencephalon via the psychoencephalic coefficient of cephalisation and from this the size of the whole brain, on the ground of the knowledge of the relation between the sizes of the psychoencephalon and the rest of the brain. Too little, however, is known of this relation between the sizes of the psychoencephalon and the rest of the brain; the data collected by DUBOIS (1897 *a*, p. 34; 1897 *b*, p. 369; 1897 *c*, p. 23; 1898, pp. 436 f.f.; 1930, pp. 256–258) at any rate are few in number. From the available data it appears, that in Chiroptera and in Older Tertiary Mammalia the metencephalon plus myelencephalon are relatively very large and that therefore the psychoencephalon must be relatively small, as compared with most Mammalia.

As regards further data about the cephalisation, we may distinguish an earlier and a later period in Dubois' papers. In his earlier publications statements are found about the coefficient of cephalisation, often running into a couple of decimals and an explanation of its value is looked for in the development of the organs of sense, the muscles, in the activity, the length of the body, *etc.*, and taking all this into consideration the conformity and the deviation of the value of the coefficient of cephalisation with respect to the place of the animal in the natural system is substantiated. In his later papers these detailed figures and the above mentioned explanations about the value of the coefficient of cephalisation are lacking; he chiefly deals with the factor of the duplication, quadruplication, *etc.*, of the cephalisation on account of cell-divisions in the brain and on the strength of this the Mammalia are systematically arranged on a scale of gradually higher stages.

In the earlier papers by Dubois the explanation of the value of the coefficient of cephalisation is founded on the degree of development of the organs of sense, the muscles, on the activity, on the length of the body, *etc.* In the following pages these matters will be dealt with more elaborately, because they are of great importance for our purpose. First a general exposition will be given, after which in the following discussion of the value of the coefficient of cephalisation in connection with the systematical place of the animal or group of animals in question, a single word in brackets will suffice to denote the cause of the value of the coefficient of cephalisation.

In the very first publications much attention is paid to the eye and its influence on the development of the brain. Later, Dubois (1913, p. 612; 1914 *a*, p. 667; 1914 *b*, p. 348) no longer attributes a high cephalisation to the development of the eye, but to that of touch, hearing, *etc.* In the same articles Dubois (1913, p. 614; 1914 *a*, p. 668; 1914 *b*, p. 350) says that the reduction of the eye is a cause of absolute diminution of the quantity of brain, as in the Anguillidae, where the reduction of the eye is a second cause of absolute diminution of the quantity of brain. But Dubois (1913, p. 614; 1914 *a*, p. 668; 1914 *b*, p. 350) adds that the influence of the not segmentally constituted eye in itself remains in all cases restricted. Even *Equus caballus* L., which possesses an absolutely larger (day-)eye than *Elephas*, rises still little above the average level of the coefficient of cephalisation for Mammalia. Nevertheless in the following this will repeatedly be pointed out as the size of the eye is of so much importance for the architecture of the skull. In these articles Dubois (1913, pp. 612, 613; 1914 *a*, pp. 667, 668; 1914 *b*, pp. 348, 349) attributes the augmentation of the quantity of brain to the sense organs of touch, hearing, smell, and the lateral line, because the surfaces of these organs of sense (in opposition to the eye, which forms definite images) increase simply proportional to the superficial dimension of the animal (consequently with the exponent of correlation 0.66 . . .). The influence of the segmentally constituted sense organs is very high; their influence can grow, as it were, endlessly with the development of "specific sense-energies" in the different segments. The tactile organs have thereby always the lead with the higher organisation of the nervous system (Dubois, 1913, p. 614; 1914 *a*, p. 668; 1914 *b*, p. 350). So Dubois was able to write (1928 *a*, p. 253; 1928 *b*, p. 305), that phylogenetically the senses of sight, smell, and hearing progress apparently concomitant with the cephalisation of the nervous system. With their larger psychoencephalon than that of the earlier forms, the phylogenetically later mammalian forms have also larger eyes, and larger olfactory receptors (we find the cribriform plate of the ethmoid bone extended, indicative of an increased number of olfactory nerve fibers). In this connection Dubois compares *Lama* with *Procamelus* and *Martes* with *Mustela*.

In his publications of 1919 Dubois demonstrates the significance of the influence of the development of the musculature on the cephalisation, but adds (1919 *a*, p. 516 foot note; 1919 *b*, p. 724 foot note) that the significance of the influence of the organs of hearing, touch and other organs of sense on the quantity of brain of *Elephas*, American Monkeys, Cetacea, Pinnipedia, Crocodilia and Pisces, all Vertebrata with a strongly developed musculature, is, however, not slight either. Dubois, however, strongly emphasizes the degree of development of the musculature as the cause of the cephalisation; this is the case, where the muscles are voluminous, strong and (or) quick; in a few cases it refers to the muscles of the head as in the case of the very voluminous muscles in the proboscis of *Elephas;* in most cases, however, it is a question of muscles of the extremities, trunk or tail as in American Monkeys, Cetacea, *Phoca*, *Otaria*, Crocodilia and Pisces (DUBOIS, 1919 *a*, pp. 516/517; 1919 *b*, pp. 724/725). In Mammalia the correlation between a great quantity of brain and great muscular force is frequently met with (DUBOIS, 1921, p. 1000; 1922 *a*, p. 1282). In the same way a relation between activity and cephalisation exists. DUBOIS (1921, p. 1003; 1922 *a*, p. 1286) mentions as example that among the Reptilia and the Amphibia the swift species have a higher cephalisation than the slow species. Thus *Hyla arborea* (L.) has double the cephalisation of *Rana temporaria* L. (*Rana fusca*).

Finally the length and the shape of the body also have an influence on the value of the coefficient of cephalisation. DUBOIS (1913, pp. 600, 613 614; 1914 *a*, pp. 654/655, 668; 1914 *b*, pp. 333/334, 349/350; 1917, p. 291) states in this connection: A great length of the body, as occurs in Anguillidae, Ophidia and *Anguis fragilis* L. is the cause of a low value of the coefficient of cephalisation. In proportion to the weight of the body, the not specialised segmental sensu-motorical unities are too equivalent for a representation in the brain, proportional to that of other Pisces and Reptilia. The body becomes thereby, as it were, to a certain amount, a ballast for the brain. This is in a more lateral sense the case in the Testudinides (Chelonia).

The above mentioned factors as the development of the eye and of the other organs of sense, the development of the musculature and its concomitant activity and lastly the length of the body, in the first place bring about the fact, that the numerical value of the coefficient of cephalisation, at any rate, of the psychoencephalic coefficient of cephalisation, shows a gradual increase corresponding with the consecutively higher orders, that the value of the coefficient of cephalisation classifies the animal species and animal groups in a satisfactory way, namely pretty well in conformity with the degree of their organisation, with the natural system and with phylogenetic considerations, not only in the Mammalia, but also in the Non-Mammalia, and that this classification – leaving aside certain exceptions to the rule – is at any rate nowhere in contradiction to the natural system. Secondly the factors summed up above give rise to the fact that some groups deviate from related groups as to the value of the coefficient of cephalisation; the best-known examples of such deviations are the Cebinae (genera *Cebus* and *Ateles*), *Elephas* and the aquatic Mammalia, but also within the Rodentia well-known exceptional cases are found, nay within every group, nay within a genus deviations occur, because the systematical groups or little groups comprise forms that are more specialised, more progressive and more highly cephalised than their nearest conservative relatives; the difference in the value of the coefficient of cephalisation can be so considerable as between the largest groups of Mammalia (Dubois, 1897 *a*, pp. 3/4; 1897 *b*, p. 337; 1897 *c*, p. 1; 1913, pp. 595, 596; 1914 *a*, pp. 649, 650; 1914 *b*, pp. 324, 325; 1918 *a*, p. 1416; 1918 *b*, p. 1328; 1920 *a*, pp. 83, 85, 86; 1924 *a*, pp. 319/320; 1924 *b*, pp. 430, 431; 1928 *a*, p. 255; 1928 *b*, p. 308; 1930, pp. 248, 253; 1934 *b*, p. 74; 1938, pp. 39, 40).

About the coefficient of cephalisation in the Pisces Dubois (1913, p. 600; 1914 *a*, pp. 654/655; 1914 *b*, pp. 333/334) mentions the following. The coefficient of cephalisation is high in *Esox lucius* L. (0.0245), *Gobio gobio* (L.) (*Gobio fluviatilis*) (0.0195), *Cyprinus carpio* L. (0.0190), *Carassius carassius* (L.) (*Carassius vulgaris*) (0.0186), *Gasterosteus aculeatus* L. (0.0179) and *Perca fluviatilis* L. (0.0153). It is low in *Conger conger* (L.) (*Conger vulgaris*) (0.0060) and especially in *Anguilla anguilla* (L.) (0.0045; great body length; reduction of the eye). In the comparatively high values of the coefficient of cephalisation most Pisces (sense lines, olfactory organ; Muraenidae excepted) equal the Reptilia (Dubois, 1913, pp. 600, 613; 1914 *a*, pp. 654, 668; 1914 *b*, pp. 333, 349; 1917, p. 293; 1919 *a*, p. 516; 1919 *b*, p. 724).

For the value of the coefficient of cephalisation in Amphibia Dubois (1913, pp. 599, 612; 1914 *a*, pp. 653/654, 667; 1914 *b*, pp. 332, 333, 348; 1917, pp. 292/293) gives the following data. A comparatively high value of the coefficient of cephalisation (calculated for $r = 0.56$) is found in *Rana esculenta* L. (0.0127), *Rana pipiens* Schreber (*Rana virescens*) (0.0138), *Alytes obstetricans* (Laur.) (0.0131), and especially *Hyla arborea* (L.) (0.0179; forefeet used as hands). This value has evidently no relation with the surroundings in which the animals live. The waterfrog *Rana catesbeiana* Shaw (0.0094) ranks near to the landfrog *Rana temporaria* L. (*Rana fusca*) (0.0095). The watersalamander *Triturus cristatus* (Laur.) (*Triton cristatus*) (0.0062) has a lower cephalisation than the landsalamander *Salamandra salamandra* (L.) (*Salamandra maculosa*) (0.0078). In general the value of the coefficient of cephalisation in Amphibia does not differ much from that of the Reptilia (Dubois, 1913, p. 599; 1914 *a*, p. 654; 1914 *b*, p. 333).

About the value of the coefficient of cephalisation in Reptilia Dubois (1913, p. 598; 1914 *a*, p. 652; 1914 *b*, p. 331) states the following. The coefficient of cephalisation (calculated for $r = 0.56$) has a low value in *Anguis fragilis* L. (0.0071–0.0082), in the Ophidia (*Naja melanoleuca* Hallow 0.0098; *Vipera berus* (L.) 0.0102) and the Testudinides (*Testudo hermanni* Gmel. (*Testudo graeca* auct. non L.) 0.0075) in contradistinction to the Lacertilia (0.0165–0.0191). The great length of the body as well as the great ballast of the body plays a part in it, as we saw in the above. The Loricata (Crocodilia) probably show a higher cephalisation (well developed organ of hearing) (Dubois, 1914 *a*, p. 668; 1914 *b*, p. 349 foot note; 1917, p. 293; 1919 *a*, p. 516; 1919 *b*, p. 724). According to Ariëns Kappers (1934, p. 463) the coefficient of cephalisation in the Reptilia is 0.019 at the utmost.

As to the value of the coefficient of cephalisation of the Aves Dubois (1913, pp. 596, 612; 1914 *a*, pp. 650, 667; 1914 *b*, pp. 328, 329, 348; 1917, p. 292) gives a list of its values and besides points out the following. The highest value of the coefficient of cephalisation is found in the Psittaci (*Amazona amazonica* (L.) = *Chrysotes amazonicus* 0.30; *Psittacula krameri* (Scop.) = *Palaeornis docilis* 0.29; "the Monkeys among Birds"; hand-like paw, pincer-like beak). The cephalisation of the Corvidae is only a little lower (0.24–0.26); the value of their coefficient of cephalisation is hardly higher than the average value in the Mammalia. The coefficient of cephalisation of the Striges is high (0.22; *Athene noctua* (Scop.) 0.22; sense of touch in the skin, quick ear). The coefficient of cephalisation of most Aves – varying from 0.105 in *Phylloscopus collybita* (Vieill.) (*Phylloscopus rufus*) to 0.17 in *Parus major* L. and *Falco tinnunculus* L. – is equal to that of the lowest cephalised Mammalia. The value of the coefficient of cephalisation in the Gallinacei and Columbae (*Pavo cristatus* L. 0.07; *Phasianus colchicus* L. 0.07; *Columba livia* (L.) dom. = *Columba domestica* 0.08) is equal to that of the Muridae. – According to Ariëns Kappers (1934, p. 463) the coefficient of cephalisation in the Aves varies from 0.045 to 0.30, *i.e.* it reaches a value equivalent to that of the Carnivora among the Mammalia.

Dubois dwells at length upon the value of the coefficient of cephalisation in the Mammalia. As we already pointed out above, his earlier publications upon this subject differ from the later ones. In his latest papers he hardly if ever gives calculations of the coefficient of cephalisation to some decimals, as they occur in his earlier publications. Indeed, he says during this transition period, that some of his earlier calculations require correction (DUBOIS, 1924 *a*, p. 321 foot note; 1924 *b*, p. 432 foot note), but he rarely gives corrected values of the coefficient of cephalisation.

Therefore we will not try and compile all the figures given by DUBOIS about the coefficient of cephalisation in the Mammalia. We will only mention those figures which DUBOIS himself remarks upon or which in his opinion can be explained on account of the development of the organs of sense, of the muscles or of the length of the body, *etc.* His publications of 1897 (1897 *a*, pp. 36–38; 1897 *b*, pp. 370-373; 1897 *c*, pp. 24-25) contain lists of the value of the coefficient of cephalisation in the Mammalia; also those of 1914 (1914 *b*, pp. 326/327; see also 1917, p. 219), whereas in his publication of 1938 (pp. 44-45) he only remarks upon similar figures stated by BRUMMELKAMP.

The following is taken from these reflections in the earlier papers of DUBOIS – up to and including those of 1921 –; as I already mentioned above, the organ of sense or the development of the muscles hold responsible for the degree of the cephalisation will be mentioned in brackets, wherever DUBOIS indicates this.

The Marsupialia (coefficient of cephalisation 0.0668) rank very low, even lower than the Rodentia (DUBOIS, 1897 *a*, p.39; 1897 *b*, p. 374; 1897 *c*, p. 26).

The Insectivora like the Marsupialia (coefficient of cephalisation of the Insectivora 0.0688–0.1874) are lower in rank than the Rodentia (DUBOIS, 1897 *a*, p. 39; 1897 *b*, p. 374; 1897 *c*, p. 26). The value of the coefficient of cephalisation in Soricidae is very low (0.06); in *Tupaia* (0.189; squirrel-like) it is trebled (DUBOIS, 1913, p. 612; 1914 *a*, p. 666; 1914 *b*, pp. 327, 348; 1917, p. 293).

Among the Chiroptera *Pteropus* (coefficient of cephalisation 0.1926) deviates considerably from the Microchiroptera (0.0431–0.0436), which have the lowest coefficient of cephalisation of all recent Mammalia examined (DUBOIS, 1897 *a*, p. 39; 1897 *b*, p. 374; 1897 *c*, p. 26). The different behaviour in this respect of Megachiroptera and Microchiroptera indicates rightly their different origin; the Megachiroptera are next in rank to the Microchiroptera, both rank under the Insectivora (DUBOIS, 1913, p. 596; 1914 *a*, p. 650; 1914 *b*, p. 325). According to this later publication of DUBOIS (1913, p. 611; 1914 *a*, p. 666; 1914 *b*, pp. 327, 347) the coefficient of cephalisation in Chiroptera is low; in Megachiroptera 0.095–0.098; in Microchiroptera still lower: 0.044–0.049.

In his earliest papers DUBOIS (1897 *a*, p. 39; 1897 *b*, p. 373; 1897 *c*, p. 26) states that the coefficient of cephalisation of the Rodentia lies between 0.0767 and 0.2369, causing part of them to rank very far below the Ungulata and the Carnivora. According to DUBOIS in his later publication (1913, pp. 611/612; 1914 *a*, p. 666; 1914 *b*, pp. 327, 347/348; 1917, pp. 291, 293) the Rodentia deviate mutually considerably in the values of their cephalisation, dependent on the development of the sense of hearing and of touch. The coefficient of cephalisation of *Rattus norvegicus* (Berkenhout) (*Epimys norvegicus* = *Mus decumanus*) (0.077), *Rattus rattus* (L.) (*Mus rattus*) (0.080) and of *Mus musculus* L. (0.078) is half that of *Lepus timidus* L. (0.168; hearing) and *Oryctolagus cuniculus* (L.) (*Lepus cuniculus*) (0.172) and only a third part of that of Sciuridae (0.240–0.242; touch). In *Jaculus* (*Dipus*) (0.167) and *Eliomys* (0.151) the organ of touch has caused the increase of the brain.

Among the Edentata *Manis* (coefficient of cephalisation 0.0837) ranks very low, still lower than the Rodentia. *Myrmecophaga* (0.2675 of 0.2193) on the other hand ranks considerably higher. Therefore a considerable difference exists between the Edentata of the Old World and of the New World (DUBOIS, 1897 *a*, p. 39; 1897 *b*, p. 374; 1897 *c*, p. 26; 1914 *b*, p. 325).

The Carnivora (coefficient of cephalisation 0.2166–0.4413) rank about as high as the Ungulata (0.2026–0.4573, except *Elephas* and *Hippopotamus*), the lower Monkeys (0.2499–0.4897) hardly exceeding them (DUBOIS, 1897 *a*, pp. 38/39; 1897 *b*, p. 373; 1897 *c*, p. 26). The coefficient of cephalisation in the Canidae (0.366–0.384; hearing, smell) is about twice as high as in the Mustelidae (0.177–0.219), with the exception of the Lutridae (0.38–0.40; *Lutra lutra* (L.) = *Lutra vulgaris* 0.400), which reaches the rank of Canidae (DUBOIS, 1913, p. 612; 1914 *a*, p. 666; 1914 *b*, pp. 326/327, 348). The coefficient of cephalisation in *Panthera leo* (L.) (*Felis leo* L.) (0.314) does not differ much from that of *Felis catus* L. (*Felis domestica* Gm.) (0.332), though the relative proportion is 5 : 1 (DUBOIS, 1914 *b*, p. 327; 1917, p. 291). The coefficient of cephalisation of the Felidae is 0.33, of the Canidae 0.37, but of *Ursus arctos* L., *Ursus horribilis* Ord, *Sele-*

narctos thibetanus (G. Cuv.) (*Ursus tibetanus*) and *Thalarctos maritimus* (Phipps) (*Ursus maritimus*) about 0.5, that of *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) 1.00 or 0.75, *i.e.*, one third higher or equal with that of the Anthropoid Apes, while the former species of Bears are on a line with *Semnopithecus*. The Ursidae are distinguished from the other terrestrial Carnivora by their very strong musculature which is especially the case in *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) (Dubois, 1921, pp. 1000, 1002; 1922 *a*, pp. 1282, 1283, 1284, 1285). – In the Pinnipedia the coefficient of cephalisation is 0.6 (*Zalophus californianus* (Less.) 0.615) (sense of hearing and of touch; small eye) and thus equal to that of Anthropoid Apes (Dubois, 1913, p. 613; 1914 *a*, pp. 667, 668; 1914 *b*, pp. 326, 349; 1917, p. 293; 1919 *a*, pp. 515/516; 1919 *b*, pp. 723/724; 1921, p. 1004; 1922 *a*, pp. 1287/1288). Dubois (1919 *a*, p. 516 foot note; 1919 *b*, p. 724 foot note) adds 0.6766 as the value of the coefficient of cephalisation of *Phoca vitulina* L. and 0.7025 of *Zalophus californianus* (Less.) (*Otaria californiana*).

As to the Cetacea Dubois states in his earlier papers (1897 *a*, p. 39; 1897 *b*, p. 373; 1897 *c*, p. 26) that the coefficient of cephalisation is relatively low (0.2263 or 0.2680), perhaps because they are ancient forms; nevertheless the coefficient of cephalisation of *Balaenoptera* is almost equal to that of the Rodentia, though *Balaenoptera* ranks very low according to the relative weight of the brain. In later publications Dubois (1913, p. 613; 1914 *a*, pp. 667, 668; 1914 *b*, pp. 326, 349; 1917, p. 293; 1919 *a*, pp. 515/516; 1919 *b*, pp. 723/724; 1921, p. 1004; 1922 *a*, pp. 1287/1288) fixes the value of the coefficient of cephalisation of the Odontoceti at 0.7 (*Phocaena phocaena* (L.) = *Phocaena communis* 0.733; *Tursiops truncatus* (Mont.) = *Tursiops tursiops* 0.981) and of the Mystacoceti at 0.4 (*Sibbaldus musculus* (L.)? = *Balaenoptera Sibbaldi* 0.397; *Balaenoptera physalus* (L.)? = *Balaenoptera musculus* 0.3841 or 0.384). The Odontoceti (highly developed sense of hearing; eye very small; sense of touch not highly developed; esp. Delphinidae very rapid swimmers with very powerful dorsal muscles) equal to the value of the coefficient of cephalisation of Anthropoid Apes and have considerably higher cephalisation than the Mystacoceti, which still possess comparatively larger brain than the Dogs.

About the Ungulata Dubois (1897 *a*, pp. 38/39; 1897 *b*, p. 373; 1897 *c*, p. 26) states in his earlier papers that these (coefficient of cephalisation 0.2026–0.4573, except *Elephas* and *Hippopotamus*) are about equal to the Carnivora (0.2166–0.4413). The Ruminantia (0.3358-0.4209) are hardly surpassed by the lower Monkeys (0.2499-0.4897). The low coefficient of cephalisation of *Tragulus* (0.2202) and of *Hippopotamus* (0.1819) perhaps may be accounted for by the fact that these genera represent very ancient forms. The coefficient of cephalisation of *Hippopotamus* approximates that of the Rodentia, though the relative brain weight of *Hippopotamus* is very low. – Among the extinct Ungulata † *Phenacodus primaevus* Cope (coefficient of cephalisation 0.0420) and † *Uintatherium mirabile* (Marsh) (*Dinoceras mirabile*) (coefficient of cephalisation about half of the latter) had a coefficient of cephalisation even lower than that of the recent Microchiroptera; † *Uintatherium* (*Dinoceras*) would have the smallest relative brain weight of all recent and fossil Mammalia (Dubois, 1897 *a*, p. 39; 1897 *b*, p. 374; 1897 *c*, p. 26). – *Elephas* takes an important place in Dubois' discussions, because of its very high coefficient of cephalisation. In his earlier papers (1897 *a*, pp. 39/40; 1897 *b*, pp. 374/375; 1897 *c*, pp. 26/27) Dubois mentions a coefficient of cephalisation of 1.2484 for *Elephas indicus* L.; this was three times as high as for the Ruminantia, which must be wrong according to Dubois at that time; it led him to the conclusion that in calculating the coefficient of cephalisation a different value of the factor of relation should be taken into account. In his later publications (1913, pp. 596, 612; 1914 *a*, pp. 650, 666; 1914 *b*, pp. 325, 326, 348; 1917, pp. 291/292; 1919 *a*, p. 515; 1919 *b*, p. 723; 1924 *a*, p. 320; 1924 *b*, p. 431) Dubois fixes the value of the coefficient of cephalisation at 1.273 (trunk: touch, chemical sense, muscles). *Elephas* surpasses the other large Ungulata (coefficient of cephalisation 0.40; *Equus caballus* L. 0.406; *Giraffa camelopardalis* (L.) (*Camelopardalis giraffa*) 0.424; *Oryx beisa* (Rüpp.) 0.427; *Alces americana* (Clinton) 0.368; *Camelus dromedarius* L. 0.362; *Hippopotamus amphibius* L. 0.185) three times in cephalisation. The Elephant ranks even much higher than the Anthropoid Apes (coefficient of cephalisation 0.75; *Pongo pygmaeus* (Hopp.) = *Simia satyrus* auct. 0.753; *Hylobates* (*Symphalangus*) *syndactylus* (Desm.) 0.770), takes its place between *Homo* and the Anthropoid Apes and differs just as greatly from his nearest relatives as Man differs from his.

As to the Primates, Dubois already states in his earlier papers

(1897 *a*, pp. 38/39; 1897 *b*, p. 373; 1897 *c*, p. 26), that *Homo* (coefficient of cephalisation 2.6778–2.8186) stands out far among the others, his cephalisation being about four times that of the Anthropoid Apes (0.6994–0.7607). These Anthropoid Apes possess only double the quantity of brain of the Carnivora (0.2166–0.4413) and Ruminantia (0.3358–0.4209), which the lower Monkeys (0.2499-0.4897) hardly surpass. In later papers DUBOIS (1913, p. 612; 1914 *a*, p. 667; 1914 *b*, pp. 325, 326, 348; 1917, pp. 291, 292; 1919 *a*, p. 515; 1919 *b*, p. 723) points out that American Monkeys, such as *Ateles* (coefficient of cephalisation 1.195; touch "hand" in their tail) and *Cebus* are higher cephalised than the Monkeys of the Old World (*Trachypithecus pyrrhus* (Horsf.) = *Semnopithecus maurus* F. Cuv. 0.489; *Macaca ira* (F. Cuv.) = *Macacus cynomolgus* 0.369), the Anthropoid Apes not excepted (*Pongo pygmaeus* (Hopp.) = *Simia satyrus* 0.753; *Hylobates* (*Symphalangus*) *syndactylus* (Desm.) 0.770). Other Platyrhina, however, have a lower coefficient of cephalisation, such as *Callithrix jacchus* (L.) (*Hapale jacchus*) (0.395) and *Leontocebus rosalia* (L.) (*Midas rosalia* L.) (0.493). In *Cebus* and *Ateles* (very lively) the coefficient of cephalisation is more than three times as high as that of *Alouatta* (*Mycetes*) (exceedingly indolent; relation to muscular power); in *Alouatta seniculus* (L.) (*Mycetes seniculus*) the coefficient of cephalisation (0.37) is about the same as that of *Macaca ira* (F. Cuv.) (*Macacus cynomolgus*) (DUBOIS, 1921, pp. 1002, 1003; 1922 *a*, pp. 1285, 1286). The ratio of cephalisation of *Cebus* and *Callithrix* (*Hapale*) is 1.8 : 1. *Cebus* has 1.5 times higher cephalisation as compared with *Saimiri* (*Chrysothrix*) (DUBOIS, 1919 *a*, p. 519; 1919 *b*, p. 727). The coefficient of cephalisation of the much quicker *Saimiri* (*Chrysothrix*) is considerably higher than that of *Leontocebus rosalia* (L.) (*Midas rosalia* L.) and *Callithrix* (*Hapale*) (DUBOIS, 1921, p. 1004; 1922 *a*, p.1287). Though the body weight of the slow *Pongo pygmaeus* (Hopp.) is certainly a third greater than that of the more muscular and very lively *Pan troglodytes* (Blumenbach), the brain weight of the two species is the same in the females, in the males that of *Pongo pygmaeus* (Hopp.) is only little more (DUBOIS, 1921, pp. 1003/1004; 1922 *a*, p. 1287). To the value of the coefficient of cephalisation of *Homo* DUBOIS reverts later on in great detail. According to DUBOIS (1913, p. 612; 1914 *a*, p. 667; 1914 *b*, pp. 326, 348; 1924 *a*, p. 320; 1924 *b*, p. 431) *Homo sapiens* L. (coefficient of cephalisation 2.818–2.822) owes his high rank to his hand. His cephalisation is almost equal to nearly four times that of Anthropoid Apes (0.753–0.770), consequently he has risen still higher above the latter than *Sciurus* above *Mus*, or *Elephas* above the other Ungulata. The relatively large encephalon of † *Homo neanderthalensis* King and among the races of modern Man that of the Mongoloids is in agreement with the development of the powerful muscle apparatus (Dubois, 1921, p. 1004; 1922 *a*, p. 1288). Dubois (1921, p. 996; 1922 *a*, p. 1280) ascribes the very high cephalisation of † *Homo neanderthalensis* King to the particularly powerful muscles and also gives indications of such a relation among human races. Elsewhere, especially in his later papers Dubois (1898, p. 441; 1913, p. 604; 1914 *a*, p. 658; 1914 *b*, pp. 337/338; 1934 *a*, pp. 189, 191/192, 193; 1938, p. 46) emphatically states that not only Germans and Englishmen have the same cephalisation, but that Europeans and Australians too have the same standard of cephalisation, in short, that the real coefficient of cephalisation of all recent human races is equal; the same applies to the real coefficient of cephalisation of both sexes. However, there are differences in the specific size of the brain, about which Dubois gives more details in his article of 1934 (1934 *a*, pp. 185, 191, 192, 193). The specific size of the brain corresponds to the absolute size of the brain E, related to ("bezogen auf") $P^{5/9}$, in which P represents the average body weight, raised to the power 5/9, *i.e.* the phylogenetic exponent of relation. Within a group of men or within a group of women the size of the brain E is on an average function of $P^{0.24}$, according to the formula $E = k.P^{0.24}$, in which the factor k stands for the specific volume of the brain ("spezifisches Gehirnvolumen"). The specific volume of the brain is characteristic for every group, *e.g.*, it is much lower in Australians than in Europeans and the Mongolians have the largest specific size of the brain, larger than Europeans, *etc.*, in spite of the equality in the real coefficient of cephalisation, yet the difference in the specific size of the brain is by no means immaterial to mankind.

In the later papers by Dubois – those since 1922 – we miss the statements calculated into some decimals about the value of the coefficient of cephalisation of the various genera, families, *etc.*; instead we read of a statement about the relations of the values of the coefficients of cephalisation expressed in whole numbers, which even enabled Dubois to classify quite a number of mammalian groups in a systematical scale according to the value of the coefficient of cephalisation. This later classification of the statements about the coefficient of cephalisation is based on the understanding meanwhile acquired by Dubois of the connection between the cephalisation and the division of nerve cells in the brain. For, according to these later papers of Dubois (1922 *b*, pp. 324, 325, 328; 1923, pp. 247, 248, 251; 1924 *a*, pp. 324-326; 1924 *b*, pp. 435-437; 1930, pp. 279/280, 281, 290; 1934 *b*, pp. 74/75) the difference in cephalisation accompanying the arising of a heteroneuric species from another should be due to the division of nerve cells in the brain, in the whole brain or at any rate in an important part of the brain; the number of nerve cells in the part of the brain in question respectively in the whole of the brain, will double itself and this will also cause a doubling of the quantity of that part of the brain respectively of the whole of the brain. This in its turn causes the coefficient of cephalisation for that part of the brain or the whole of the brain to be doubled. As regards the part of the brain that undergoes the doubling of the number of nerve cells and at the same time of its own quantity of brain, Dubois' papers show a great many different opinions. In his former publication (1922 *b*, p. 325; 1923, p. 248) Dubois says that in related, but heteroneuric species the coefficients of cephalisation, in many cases, are to each other as 1, 2, 3, 4. Pointing at the differences in cephalisation Dubois (1924 *a*, p. 321; 1924 *b*, p. 432; see also 1924 *a*, pp. 324-326; 1924 *b*, pp. 435-437) says, that the deviations consist in doubling of the whole or of a very great part (half) of the brain quantity calculated for equal body weight. These quantities are, therefore, mostly to each other as 1 : 2 : 4, but sometimes as 1 : 1½ : 3 : 6. In most cases doubling of the cerebrum and the cerebellum takes certainly place, whereas some of the brain parts, of small volume, perhaps do not participate in the increase. That in most cases the increase remains slightly below the relations mentioned is probably to be accounted for in this way. Dubois (1928 *a*, p. 256; 1928 *b*, p. 309; 1930, p. 259) says that slight deviations from the regular, simple relations of a geometrical progression, as well as differences between groups that are not specialized to the same degree (*e.g.*, Canidae and Felidae) are apparently based on minor peculiarities of the cerebrum of these groups. Thus, in the Canidae the rhinencephalon is doubled when comparing them with the Felidae. Comparing *Elephas* with the rest of the Ungulata we find a doubled cerebellum. The relations between the in a sense linear nearest related groups, such as Man and Anthropomorphae, Dipodidae and Muridae, even between Man and primitive Insectivora, can either be expressed in whole numbers or in simple fractions. In this publication of 1930 where Dubois draws attention to the coefficient of cephalisation of the whole brain, but especially emphasizes the coefficient of cephalisation of the psychoencephalon, which in his opinion is very important, he says (1930, pp. 260, 281, 284) that the exponent of the geometrical progression is exactly 2 and that the psychoencephalon phylogenetically grows by jumps, while the quantity doubles itself. In 1934 Dubois (1934 *b*, p. 74) adds that the coefficient of cephalisation increased, "at least approximately", in a geometrical progression of the term 2, by doubling or repeated doubling. In his paper of 1938 (pp. 39, 41) Dubois says that in 1924 it could only be stated that the deviations from a general sequence of the coefficients of cephalisation are "mostly" founded on duplication or quadruplication of these coefficients; now it is apparent that in recent and fossil Mammalia, the deviating quantities of the brain "always" – according as the available data make it certain or very probable – are to each other as the numbers 1 : 2 : 4 : 8, as the terms therefore of a geometrical series with the ratio 2. In spite of certain criticisms Dubois sticks to this value of the ratio and opines that also some cases of microcephalia vera fit in here. So it can be said, as Dubois (1928 *a*, p. 257; 1928 *b*, pp. 310/311) had observed before, that the coefficients of cephalisation of related, heteroneuric species appear to increase exactly or very nearly by duplication, quadruplication, octuplication. – The reason why the relative volume of the brain increases in its phylogenesis in the regular proportion of the terms of a geometrical series with the ratio 2, lies in the fact that the division of the brain cells is a repeated division into two which is entirely restricted to the embryonal period of life (Dubois, 1928 *a*, p. 253; 1928 *b*, p. 305; 1930, p. 290). This involves that no gradual transition in this respect is possible in the establishment of a new, heteroneuric species, but that the transition must be sudden (Dubois, 1928 *a*, pp. 258/259; 1928 *b*, pp. 312/313, 313/314). Already before Dubois (1922 *b*, pp. 308/309; 1923, pp. 231/232) had pointed out that this sudden, at all events comparatively rapid increase of the volume of the brain in the classes of Reptilia, Aves and Mammalia is very remarkable. Another remarkable fact is that in the Hominides the brain immediately possessed the same volume already in the earliest of the known crania as in modern ones. Thus there was no gradual increase of the volume of the brain and the transition from such a volume of brain as that of the Anthropoid Apes to the modern human volume seems at all events to have been a rapid one, and halfway there is still that of † *Pithecanthropus.* In phylogenesis there were according to Dubois (1922 *b*, p. 328; 1923, p. 251) long interruptions and long intervals, hence great differences in the brain quantities. In this way it can also be explained how, as Dubois (1897 *a*, p. 3; 1897 *b*, p. 337; 1897 *c*, p. 1) observes, the Mammalia show a development of the brain which climbs the scale with the orders and which is only acquired by them by degrees. Within the Mammalia we find an ever increasing development of the brain during the Kainozoicum; there exists an increase of the size of the prosencephalon between mammalian species of Early Tertiary and of recent times, belonging to the same group, of which the earlier discussed general law of brain growth of O. C. Marsh tried to give an analysis and a formulation (Dubois, 1920 *a*, p. 82; 1928 *a*, pp. 253/254/255; 1928 *b*, pp. 306/307/308; 1930, p. 248).

The value of the coefficient of cephalisation also bears a relation to the size of the body. Most of the heteroneuric species with low cephalisation are small, in comparison with the allied species with high cephalisation. This proves that the phylogenetic growth of the brain in which – different from what is found in the establishment of a new homoneuric species – certain parts of this organ increase to a greater degree than the other parts, and accordingly a heteroneuric species originates, is probably always too accompanied with increase of the bulk of the body. Only with the same increase of the bulk of the body, the increase of the volume of the brain is comparatively greater than in the establishment of a new homoneuric species (Dubois, 1922 *b*, pp. 325/326; 1923, pp. 248/249). In a later paper where sequences are drawn up, of which, however, the species, genera and higher groups are not to be considered as direct ancestors of one another, Dubois (1928 *b*, pp. 311-312) observes that in consequence the lower forms are seldom of smaller size than those on a higher level of cephalisation, and this easily may be conceived, since, *e.g.*, in such a homomorphous genus as "*Felis*", the weights of the species diverge in the ratio 1 : 100, and this divergence is still greater between Mammalia belonging to different genera and of more distant kinship. In this way the lower form *Hippopotamus* may be much larger (indeed 10 times heavier) than the higher form *Choeropsis*.

Now, on the ground of the acquired understanding of the connection between the cephalisation and the division of nerve cells in the brain, Dubois sets up in his later publications – those from 1922 onward – sequences of genera of Mammalia and classifies genera, small groups and groups of Mammalia in a scale according to the value of the coefficient of cephalisation. In his paper of 1930 (p. 258; see also 1928 *a*, pp. 255/256; 1928 *b*, p. 309) Dubois gives such a scale. In the following pages we shall combine this scale with the table of the geometrical progression of the psychocephalisation given by Dubois (1928 *a*, p. 258; 1928 *b*, p. 312) and at the same time include the numerous cases mentioned by Dubois in the text of his later publications. Such a tabular survey will answer our purposes, namely to give an insight in the factors affecting the size of the brain and through this, the size of the cerebral capsule.

This scale then, will look as follows:

Stage 7: absolute value of the coefficient of cephalisation ± 2.5; relative value of the coefficient of cephalisation in relation to *Homo* 1.

Primates: *Homo sapiens* L. and as these are all existing groups of human beings of either sex (Dubois, 1930, p. 258; 1934 *a*, pp. 189, 193; see also 1924 *a*, p. 324; 1924 *b*, p. 435; 1928 *a*, p. 258; 1928 *b*, p. 312). Coefficient of cephalisation of the European fully 2.5 (Dubois, 1930, p. 267) and upwards of 2.8 (Dubois, 1938, p. 39).
† *Homo neanderthalensis* King (Dubois, 1934 *a*, p. 193).

Stage 6: absolute value of the coefficient of cephalisation ± 1.25; relative value of the coefficient of cephalisation in relation to *Homo* 1/2.

Primates: † *Pithecanthropus erectus* (Dubois) (Dubois, 1930, pp. 266, 267, 270; 1934 *b*, p. 75; see also 1922 *b*, p. 309; 1923, p. 232; 1924 *a*, p. 324; 1924 *b*, p. 435; 1928 *a*, p. 258; 1928 *b*, p. 312). Coefficient of cephalisation 1.25 (Dubois, 1930, p. 267).
Not a single living Mammal (Dubois, 1930, p. 258).

Stage 5: absolute value of the coefficient of cephalisation ± 0.62; relative value of the coefficient of cephalisation in relation to *Homo* 1/4. Two groups have to be distinguished in this stage.

I. One group with a somewhat higher value of the coefficient of cephalisation, that is absolute value of the coefficient of cephalisation ± 1.00; relative value of the coefficient of cephalisation in relation to *Homo* 2/5.

Primates: perhaps *Cebus*, for instance *Cebus capucinus* (L.) (tail, hand) and perhaps *Ateles* (hand less perfect, perfect tail) (DUBOIS, 1930, pp. 259, 281; 1934 *b*, p. 75; 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, pp. 322, 323, 324; 1924 *b*, pp. 433, 434, 435; 1928 *a*, p. 258; 1928 *b*, p. 312).
Ungulata: perhaps *Elephas*, for instance *Elephas maximus* L. (perfect feeler and prehensile apparatus with finger in its proboscis) (DUBOIS, 1930, pp. 259, 273; see also 1924 *a*, pp. 322, 323; 1924 *b*, pp. 433, 434; 1928 *a*, p. 258; 1928 *b*, p. 312). Coefficient of cephalisation of *Elephas maximus* L. 0.9737 (DUBOIS, 1930, p. 273).
Cetacea: perhaps Delphinoceti (most perfectly specialised swimmers) (DUBOIS, 1924 *a*, pp. 322, 323; 1924 *b*, pp. 433, 434) (cf. group II).

II. Another group having the average value of the coefficient of cephalisation of this stage.

Primates: Pongidae (Anthropomorphae, Anthropoidae, Simiidae), such as *Gorilla gorilla* (Savage & Wyman), *Pan troglodytes* (Blumenbach) and *Pongo pygmaeus* (Hopp.) and the Hylobatidae (hand, visual sense, no tail) (DUBOIS, 1930, pp. 258, 270; 1934 *b*, pp. 74, 75; 1938, p. 40; see also 1924 *a*, p. 324; 1924 *b*, p. 435; 1928 *a*, pp. 255/256, 258; 1928 *b*, pp. 309, 312). Coefficient of cephalisation of the Pongidae (Anthropomorphae) upwards of 0.7 (DUBOIS, 1938, p. 39).
Nemestrinus nemestrinus (L.) (*Macacus nemestrinus*) (DUBOIS, 1930, p. 259).
Carnivora: perhaps *Helarctos malayanus* (Raffl.) (very quick climber) (DUBOIS, 1930, p. 259; 1938, p. 40; see also 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, p. 258; 1928 *b*, p. 312).
Cetacea, probably Odontoceti (DUBOIS, 1930, p. 259) (cf. group I).

Stage 4: absolute value of the coefficient of cephalisation ± 0.31; relative value of the coefficient of cephalisation in relation to *Homo* 1/8. In this stage we shall have to distinguish three groups.

I. One group with a somewhat higher value of the coefficient of cephalisation that is absolute value of the coefficient of cephalisation ± 0.45; relative value of the coefficient of cephalisation in relation to *Homo* somewhat higher than 1/8.

Primates: perhaps *Saimiri sciureus* (L.) (*Chrysothrix sciurea*) (genuinely simian) (DUBOIS, 1930, pp. 259, 281; 1934 *b*, p. 75; 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, pp. 323/324; 1924 *b*, pp. 434/435; 1928 *a*, p. 258; 1928 *b*, p. 312).
Ungulata: Bovidae (Cavicornia) and Cervidae (Cervicornia), also Giraffidae, so the Pecora excluding the Tragulidae (DUBOIS, 1930, pp. 258, 260; 1934 *b*, p. 74; 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*

p. 323; 1924 *b*, p. 434; 1928 *a*, pp. 255/256, 258; 1928 *b*, pp. 309, 312). Sometimes the Ruminantia in general are also placed here (DUBOIS, 1934 *b*, p. 75; see also 1922 *b*, p. 325; 1923, p. 248). Coefficient of cephalisation of the true Ruminantia about 0.4 (DUBOIS, 1938, p. 39).

perhaps Equidae and perhaps Rhinoceros also (DUBOIS, 1930, p. 265; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 323; 1924 *b*, p. 434; 1928 *a*, p. 258; 1928 *b*, pp. 311; 312). Coefficient of cephalisation of *Equus caballus* L. 0.40, of *Equus* (*Asinus*) *asinus* L. 0.45 and of *Equus* (*Hippotigris*) *zebra* L. and *quagga* Bodd. 0.50 (DUBOIS, 1930, p. 265).

Carnivora: Canidae (DUBOIS, 1930, p. 258; see also 1928 *a*, pp. 255/256; 1928 *b*, p. 309).

perhaps *Ursus* (climber, podochire) or the Ursidae, except *Helarctos* (DUBOIS, 1930, p. 259; 1938, p. 40; see also 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, p. 258; 1928 *b*, p. 312).

perhaps Pinnipedia (perfect specialisation for aquatic life) (DUBOIS, 1924 *a*, p. 322; 1924 *b*, p. 433).

II. Another group with a somewhat lower value of the coefficient of cephalisation, that is absolute value of the coefficient of cephalisation ± 0.25; relative value of the coefficient of cephalisation in relation to *Homo* somewhat lower than 1/8.

Carnivora: Felidae (DUBOIS, 1930, p. 258; 1934 *b*, p. 74; 1938, p. 39; see also 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, pp. 255/256; 1928 *b*, p. 309). Coefficient of cephalisation of *Felis* 0.33 (DUBOIS, 1938, p. 39).

III. A third group for which it has not been indicated more precisely whether and how far the coefficient of cephalisation deviates from the average proper to this stage.

Ungulata: *Choeropsis* (DUBOIS, 1930, pp. 259/260; 1934 *b*, p. 75; 1938, p. 40; see also 1928 *a*, p. 258; 1928 *b*, p. 312).

perhaps *Sus* (higher in motive respect than *Hippopotamus*) (DUBOIS, 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 323; 1924 *b*, p. 434).

perhaps *Tayassu* (*Dicotyles*) (DUBOIS, 1930, p. 271).

perhaps *Tapirus terrestris* (L.) (DUBOIS, 1930, p. 271; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *b*, p. 434).

Cetacea: Mystacoceti (much less good swimmers than Delphinoceti) (DUBOIS, 1930, p. 259; see also 1924 *a*, pp. 322/323; 1924 *b*, pp. 433/434).

Carnivora: *Martes*, *e.g.*, *Martes martes* (L.) (*Mustela martes*) (very agile) and *Martes foina* (Schreb.) (*Mustela foina*) (very agile) and *Lutra* (swimmer) (DUBOIS, 1930, p. 259; 1934 *b*, p. 75; 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, pp. 257, 258; 1928 *b*, pp. 310, 312).

Rodentia: perhaps the typical or arboreal Squirrels and flying Squirrels, *e.g.*, *Sciurus* (agile, uroptere, podochire) (DUBOIS, 1934 *b*, p. 75; 1938, pp. 39, 40; 1939, pp. 125, 126; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 323; 1924 *b*, p. 434). Coefficient of cephalisation of these Squirrels 0.24 or about 0.245 (DUBOIS, 1938, p. 39; 1939, p. 125).

Stage 3: absolute value of the coefficient of cephalisation ± 0.15; relative value of the coefficient of cephalisation in relation to *Homo* 1/16. Three groups have to be distinguished in this stage.

I. One group with a somewhat higher value of the coefficient of cephalisation, that is absolute value of the coefficient of cephalisation ± 0.2; relative value of the coefficient of cephalisation in relation to *Homo* somewhat higher than 1/16.

Primates: perhaps *Callithrix jacchus* (L.) (*Hapale jacchus*) (more squirrel-like than simian) (Dubois, 1930, pp. 259, 281; 1934 *b*, p. 75; 1938, pp. 40, 45; see also 1924 *a*, pp. 323/324; 1924 *b*, pp. 434/435; 1928 *a*, p. 258; 1928 *b*, p. 312).

Ungulata: Tragulidae (stealthily moving) (Dubois, 1930, pp. 258, 260; 1934 *b*, p. 75; 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 323; 1924 *b*, p. 434; 1928 *a*, pp. 257, 258; 1928 *b*, pp. 310, 312).

perhaps † *Mesohippus bairdii* Leidy (Dubois, 1930, p. 265; see also 1928 *a*, p. 258; 1928 *b*, p. 312). Coefficient of cephalisation 0.2486–0.2503 (Dubois, 1930, p. 265).

perhaps *Procavia* (*Hyrax*) (Dubois, 1924 *a*, pp. 321, 323, 324; 1924 *b*, pp. 432, 434, 435).

perhaps † *Arsinoitherium* (Lower Oligocene) (Dubois, 1930, p. 273; see also 1928 *b*, p. 312). Coefficient of cephalisation 0.1895 (Dubois, 1930, p. 273).

Carnivora: Viverridae (Dubois, 1930, p. 258; see also 1924 *a*, p. 322; 1924 *b*, p. 433).

II. Another group with a slightly lower value of the coefficient of cephalisation, that is absolute value of the coefficient of cephalisation ± 0.12; relative value of the coefficient of cephalisation in relation to *Homo* somewhat lower than 1/16.

Rodentia: Leporidae (fast runners) (Dubois, 1930, p. 258; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 323; 1924 *b*, p. 434; 1928 *a*, pp. 255/256, 258; 1928 *b*, pp. 309, 312). Coefficient of cephalisation 0.17 (Dubois, 1938, p. 39).

Dipodidae (fast runners) (Dubois, 1930, p. 258; see also 1924 *a*, p. 323; 1924 *b*, p. 434; 1928 *a*, p. 258; 1928 *b*, p. 312).

III. A third group for which it has not been indicated more precisely whether and how far the coefficient of cephalisation deviates from the average belonging to this stage.

Primates: perhaps *Tarsius* (Dubois, 1930, p. 260).

Ungulata: *Hippopotamus* (Dubois, 1930, pp. 259/260; 1934 *b*, p. 75; 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248; 1928 *a*, p. 258; 1928 *b*, p. 312).

Carnivora: *Putorius*, *e.g.*, *Putorius putorius* (L.), *Mustela erminea* L. (*Putorius ermineus*) and *Mustela nivalis* L. (*Putorius nivalis*), *Mustela*, *Meles* and *Gulo* (Dubois, 1930, p. 259; 1934 *b*, p. 75; 1938, p. 40; see also 1922 *b*, p. 325;

1923, p. 248; 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, pp. 257, 258; 1928 *b*, pp. 310, 312).

Rodentia: perhaps terrestrial Squirrels and "Marmots" (DUBOIS, 1934 *b*, p. 75; 1938, p. 40).

Chiroptera: Megachiroptera (podochire, excellent optical sense) (DUBOIS, 1930, p. 260; 1934 *b*, p. 75; see further 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, p. 258; 1928 *b*, p. 312).

Insectivora: *Tupaia* (uroptere, podochire, highly organised optical sense) (DUBOIS, 1930, p. 260; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, pp. 257, 258; 1928 *b*, pp. 310, 312).

Stage 2: absolute value of the coefficient of cephalisation ± 0.08; relative value of the coefficient of cephalisation in relation to *Homo* 1/32. Three groups have to be distinguished.

I. One group with a somewhat higher value of the coefficient of cephalisation, that is absolute value of the coefficient of cephalisation somewhat higher than ± 0.08; relative value of the coefficient of cephalisation in relation to *Homo* a little higher than 1/32.

Dermoptera: Galeopithecidae (parachute-like expansion of the skin) (DUBOIS, 1930, pp. 258, 260; see also 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, p. 258; 1928 *b*, p. 312).

II. Another group with a somewhat lower value of the coefficient of cephalisation, that is absolute value of the coefficient of cephalisation a little lower than ± 0.08; relative value of the coefficient of cephalisation in relation to *Homo* somewhat lower than 1/32.

Rodentia: Myoidea (DUBOIS, 1924 *a*, p. 323; 1924 *b*, p. 434).
  Muridae (DUBOIS, 1930, p. 258; 1934 *b*, p. 74; see also 1922 *b*, p. 325; 1923, p. 248; 1928 *a*, pp. 255/256, 258; 1928 *b*, pp. 309, 312).

Insectivora: Talpidae, such as *Talpa* (spade-like hands) and *Desmana moschata* (Pall.) (*Myogale moschata*) (swimming, proboscis) (DUBOIS, 1930, pp. 258, 260; 1934 *b*, p. 75; 1938, p. 40; see also 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, p. 258; 1928 *b*, p. 312).
  Soricidae, such as *Nectogale* (DUBOIS, 1938, p. 40).
  Erinacinae, such as *Erinaceus* and *Gymnura* (DUBOIS, 1930, pp. 258, 260; 1938, p. 40; see also 1928 *a*, p. 258; 1928 *b*, p. 312).
  Potamogalinae, such as *Potamogale* (oar tail) (DUBOIS, 1930, pp. 258, 260; 1938, p. 40; see also 1924 *a*, p. 322; 1924 *b*, p. 433; 1928 *a*, p. 258; 1928 *b*, p. 312).

III. A third group, for which it has not been indicated more precisely, whether and how far the coefficient of cephalisation deviates from the average proper to this stage.

Ungulata: perhaps † *Moeritherium lyonsi* Andrews (Upper Eocene) (DUBOIS, 1930, pp. 272/273; see also 1924 *a*, p. 323; 1924 *b*, p. 434; 1928 *a*, pp. 257/258; 1928 *b*, pp. 311, 312). Coefficient of cephalisation 0.1219 (DUBOIS, 1930, pp. 272/273).
perhaps † *Palaeosyops leidyi* Osb. (Middle Eocene) (DUBOIS, 1930, pp. 270/271; see also 1928 *a*, p. 258; 1928 *b*, p. 312).
perhaps † *Anoplotherium communis* Cuv. (Upper Eocene) (DUBOIS, 1930, p. 271).
perhaps † *Diplobune bavaricum* O. Fraas (Lower Oligocene) (DUBOIS, 1930, p. 271). Coefficient of cephalisation 0.07 (DUBOIS, 1930, p. 271).
Chiroptera: Phyllostomatidae, such as *Vampyrus* (DUBOIS, 1930, p. 260; 1934 *b*, p. 75; 1938, p. 40; see also 1928 *a*, p. 258; 1928 *b*, p. 312).
perhaps the Megachiroptera (DUBOIS, 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248). See also stage 3 group III.

Stage 1: absolute value of the coefficient of cephalisation ± 0.04; relative value of the coefficient of cephalisation in relation to *Homo* 1/64.

Ungulata: † *Uintatherium mirabile* (Marsh) (Middle Eocene) (DUBOIS, 1930 pp. 271/272; see also 1928 *a*, p. 257; 1928 *b*, p. 311). Coefficient of cephalisation 0.041 (DUBOIS, 1930, pp. 271/272).
† *Coryphodon hamatum* Marsh (Lower Eocene) (DUBOIS, 1930, p. 272; see also 1928 *a*, p. 257; 1928 *b*, p. 311). Coefficient of cephalisation 0.039 (DUBOIS, 1930, p. 272).
† *Phenacodus primaevus* Cope (Lower Eocene) (DUBOIS, 1930, p. 272; see also 1928 *a*, p. 257; 1928 *b*, p. 311). Coefficient of cephalisation 0.039 (DUBOIS, 1930, p. 272).
Carnivora: † *Arctocyon primaevus* Blainv. (Old Eocene or Upper Paleocene) (DUBOIS, 1930, pp. 273/274; see also 1924 *a*, p. 321; 1924 *b*, p. 432). Coefficient of cephalisation 0.0397 (DUBOIS, 1930, pp. 273/274).
Chiroptera: most Microchiroptera (DUBOIS, 1930, pp. 258, 260; 1934 *b*, p. 75; 1938, p. 40; see also 1924 *b*, p. 433; 1928 *a*, pp. 255/256, 258; 1928 *b*, pp. 309, 312).
Insectivora: Soricidae, such as *Sorex* and *Crocidura* (DUBOIS, 1930, pp. 258, 260; 1934 *b*, p. 75; 1938, p. 40; see also 1922 *b*, p. 325; 1923, p. 248; 1924 *a*, p. 321; 1924 *b*, p. 432; 1928 *a*, pp. 255/256, 258; 1928 *b*, pp. 309, 312). Coefficient of cephalisation 0.05 (DUBOIS, 1938, p. 39).
Centetidae (DUBOIS, 1930, pp. 258, 260; 1938, p. 40; see also 1928 *a*, pp. 255/256, 258; 1928 *b*, pp. 309, 312).

We already saw above that DUBOIS considers the small deviations from the regular, simple relations of the geometrical progression to be due to secondary variations in the cerebellum, and in the prosencephalon. Domestication too, causes a deviation, namely a reduction of the coefficient of cephalisation. Whereas the coefficient of cephalisation of *Fennecus zerda* (Zimm.), *Vulpes vulpes* (L.) and *Canis lupus* L. is 0.41, that of *Canis fami-*

liaris L. is only 0.385, so 6 % lower than the rest of the Canidae (Dubois, 1922 *b*, pp. 319/320; 1930, p. 253 foot note). But the cephalisation of *Thos aureus* (L.) is a little higher than that of *Vulpes vulpes* (L.) and of *Canis lupus* L.; *Canis lupus* L. is about equal in its cephalisation with *Vulpes vulpes* (L.) (Dubois, 1922 *b*, p. 320 foot note; 1922 *c*, p. 317; 1923, p. 243 foot note).

When checking the stages to which related forms belong, it appears that not a few species are seen to fall outside their order, family or genus, and this with a value of the coefficient of cephalisation which is double or fourfold that of their nearest relations. A single recent form (*Tragulus*) is seen falling outside the series with half the coefficient of cephalisation of its nearest relations (Dubois, 1928 *a*, p. 257; 1928 *b*, p. 310; 1930, p. 259). There are cases in which with the transition from the old to the new, more or less related forms, the coefficient of cephalisation is quadrupled or even octupled; the Mammalia concerned are generally from the oldest Tertiary, some were still living in the Oligocene (Dubois, 1930, p. 270). Further than the fourth term († *Moeritherium* to *Elephas*) the geometrical series is not continued, but undoubtedly the cephalisation of some Lower Eocene Ungulata was still less than 1/8 of that of their far relatives of recent times (Dubois, 1928 *a*, p. 257; 1928 *b*, p. 311).

It is sometimes not immaterial for the ratio of the value of the coefficient of cephalisation whether it is determined for the whole of the brain rather than for the psychoencephalon. In this connection Dubois (1928 *a*, p. 257; 1928 *b*, p. 310) mentions that the Megachiroptera show 4 times the coefficient of cephalisation by comparison of the prosencephalon, but 3 times the coefficient of cephalisation by comparison of the whole encephalon of the value of the coefficient of cephalisation of most Microchiroptera.

A number of proportions of the value of the coefficient of cephalisation of related forms, mentioned by Dubois, could not be inserted by me in the above table of stages, at least not to a certainty. A description of them may follow here.

† *Pithecanthropus* possessed two thirds of the cerebral volume of the Australian aboriginal of the same body size (Dubois, 1922 *b*, p. 309; 1923, p. 232). The coefficient of cephalisation of the Anthropoid Apes is twice that of the Old World Monkeys and Baboons (Dubois, 1922 *b*, p. 325; 1923, p. 248). According to a later publication of Dubois, however, the coefficient of cephalisation of the Cercopithecidae is little less than

0.6, whereas that of the Anthropomorphae is upwards of 0.7 (Dubois, 1938, p. 39). In another publication Dubois (1924 *a*, p. 324; 1924 *b*, p. 435) says, that the coefficient of cephalisation in the Anthropomorphae is 1½ times as great as in the Cynopithecidae; the ratio of the value of the coefficient of cephalisation of *Homo* to that in the Cynopithecidae is 6 : 1. Between *Alouatta* and *Cebus* the ratio is 1 : 3 (Dubois, 1924 *a*, p. 324; 1924 *b*, p. 435). *Lemur* possesses the sixfold coefficient of cephalisation of the primitive Insectivora (Dubois, 1924 *a*, p. 323; 1924 *b*, p. 434). *Daubentiona* (*Chiromys*) (fingers) reaches double the coefficient of cephalisation of *Lemur* (Dubois, 1924 *a*, p. 323; 1924 *b*, p. 434; 1928 *a*, p. 258; 1928 *b*, p. 312; 1930, p. 259; 1938, p. 40). The coefficient of cephalisation of *Tarsius* is at most equal to that of *Nycticebus*, perhaps only 2/3 of it (Dubois, 1924 *a*, p. 323; 1924 *b*, p. 434).

Sirenia (aquatic Mammalia) reach 1½ times the value of the coefficient of cephalisation of † *Moeritherium* (Dubois, 1924 *a*, p. 323; 1924 *b*, p. 434).

Lama guanicae (Müller) (*Lama huanachus* Molina) has twice the value of the coefficient of cephalisation of † *Procamelus gracilis* Leidy of the same size and general build (Dubois, 1928 *a*, p. 258; 1928 *b*, pp. 311, 312; 1934 *b*, p. 75). † *Merycoidodon* (*Oreodon*) has half the value of the coefficient of cephalisation of *Tayassu* (*Dicotyles*) (Dubois, 1928 *a*, p. 258; 1928 *b*, p. 312).

The cephalisation of † *Proviverra cayluxi* Filhol (psychoencephalic coefficient of cephalisation 0.1101) is half that of *Paradoxurus hermaphroditus musanga* (Raffl.) (psychoencephalic coefficient of cephalisation 0.2203) (Dubois, 1928 *a*, p. 258; 1928 *b*, p. 312; 1930, pp. 265/266). The coefficient of cephalisation of *Latax* is 1½ times that of *Lutra* (Dubois, 1924 *a*, p.322; 1924 *b*, p. 433).

Orycteropus and *Myrmecophaga* have a coefficient of cephalisation 1½ times as great as that of *Bradypus* and 3 times that of *Manis* (Dubois, 1924 *a*, p. 323; 1924 *b*, p. 434). The coefficient of cephalisation of *Manis javanica* Desm. has half the value of that of *Smutsia gigantea* (Ill.) (*Manis gigantea*) and of *Uromanis longicaudata* (Briss.) (*Manis tetradactyla*) (Dubois, 1928 *a*, p. 258; 1928 *b*, p. 312; 1930, p. 260). *Smutsia* has twice the coefficient of cephalisation of *Manis* (Dubois, 1938, p. 40).

Dolichotis (fast runner) and *Hydrochoerus* (swimmer) reach 1½ times the value of the coefficient of cephalisation of the wild

Cavia species (Dubois, 1924 *a*, p. 323; 1924 *b*, p. 434). According to a later paper of Dubois, however, *Dasyprocta*, *Hydrochoerus* and *Dolichotis* have twice the coefficient of cephalisation of *Cavia* (Dubois, 1938, p. 40).

Let us now pass on to a direct comparison of the values of the coefficient of cephalisation in the different classes of Vertebrata. Reliable data were collected above, according to which the coefficient of cephalisation varied between the values given below:

Pisces 0.0045 – 0.0245;
Amphibia 0.0062 – 0.0179;
Reptilia 0.0071 – 0.0191;
Aves 0.045 – 0.30;
Mammalia 0.039 – 2.8.

According to Dubois (1920 *a*, p. 82) "the relative volume" of the brain – in this connection meant as the cephalisation – develops within the class of the Reptilia (when the lowest fossils are included) to the eight or tenfold.

In general therefore, the cephalisation increases from the Pisces to the Mammalia (Dubois, 1920 *a*, p. 82). This is especially due to the increase of the size of the prosencephalon in the series of the Vertebrata, from the Pisces to the Mammalia (Dubois, 1928 *a*, pp. 253/254; 1928 *b*, p. 306). No definite regularity, however, is to be discovered in this progression from one class of the Vertebrata to the other. As Dubois (1918 *a*, p. 1416; 1918 *b*, p. 1328) says: in the different classes of Vertebrata the proportionality of the quantity of brain to the body weight varies greatly and is unequal. It is quite obvious, however, that the Mammalia possess a much larger and a more highly organised brain than all other animals (Dubois, 1897 *a*, p. 3; 1897 *b*, p. 337; 1897 *c*, p. 1).

We may add a few illustrative comparisons of animals from different classes with equal body weight, mentioned by Dubois (1920 *a*, p. 83). *Parus major* L., of equal body weight as *Lacerta viridis* (Laur.), has eight times the quantity of brain. *Mustela nivalis* L., of equal body weight as *Perca fluviatilis* L., has twelve times its weight of the brain.

d. The shape of the brain

It is obvious that the general shape of the brain is of great importance for the general shape of the cerebral capsule and consequently for the relative position of orbita, upper jaw, *etc.*,

etc. For the general shape of the brain the length-width-index of the brain is a good measure. The length-width-index of the brain is connected with a number of factors, such as the size of the animal, the cephalisation of the brain, the development of the olfactory sense, the size of the eye and the nature of the movement of the animal in its surroundings (HALLER VON HALLERSTEIN, 1934, pp. 184, 185, 192).

In large animals the brain is usually relatively broader than in small animals of the same group with equal or similar brain structure (ARIËNS KAPPERS according to HALLER VON HALLERSTEIN, 1934, p. 185). According to DUBOIS (1917, p. 287) the brain of a large specimen of *Canis familiaris* L. of 35 kilograms body weight, compared with that of a small specimen of 6 kilograms, is somewhat more oblong in shape; the explanation must be sought in the difference in proportion between the contents and the surface of a sphere and of a cylinder. The telencephalon of larger animals is according to ARIËNS KAPPERS (HALLER VON HALLERSTEIN, 1934, p. 185) in case of an equal or similar cephalisation ("Gliederung") usually more dolichocephalic than that of smaller animals of the same group.

Within the same group the more strongly cephalised brain is proportionately broader than the less differentiated one. The length-width-index of the brain of microsmatic Mammalia is very high according to ARIËNS KAPPERS, for instance in *Phocaena phocaena* (L.) (*Phocaena communis*) 160, in *Phoca vitulina* L. 116.9, whereas it is 74 for the German Bulldog. Among the Aves *Apteryx* has the narrowest brain, while the "Kakadu" in which a bulbus olfactorius is lacking, has a relatively very broad brain. As to the Seal, the short and broad shape of the brain can also be explained by the largeness of the eyes. According to RIESE the telencephalon of animals from all classes, moving rapidly and deftly ("gewandt") in the air or in the water is broad and almost transversally oval; this is found in the Pisces and the Aves. In the Mammalia in general the telencephalon is longitudinally oval, whereas in the Cetacea and Chiroptera it is transversally oval. In embryonic and new-born Mammalia the brain is proportionally broader than in adults, for example the width-length-index is for new-born and adult *Sus scrofa* L. 91.4 and 81 respectively and for new-born and adult *Felis catus* L. (*Felis domestica*) 105 and 93 respectively (ARIËNS KAPPERS according to HALLER VON HALLERSTEIN, 1934, pp. 184/185).

e. The size of the cerebral capsule

Whereas the number of data about the size of the brain is remarkably numerous, the direct data about the size of the cerebral capsule are few in number. The above collected data about the size of the brain, however, enable us to make many inferences about the size of the cerebral capsule, provided we bear in mind the earlier remarks about a locally and totally thickened wall of the cerebral skull and about a too spacious cavity of the cerebral capsule for the brain (too spacious for the relatively small brain), which may cause an important difference between the size of the cerebral capsule and the size of the cerebral skull (outside measurement), respectively between the size of the brain and that of the cavity of the cerebral capsule.

In the Mammalia the brain is closely conform to the wall of the cerebral capsule, so that DUBOIS, as we already saw above, thinks a determination of the volume and the weight of the brain from the capacity of the cerebral cavity for the brain more reliable than a direct determination from the brain itself. Especially for Man conversion percentages have been determined concerning this point. It may be assumed, however, that the densities of the brain in different Mammalia are pretty well equal, as the densities of the airless body, and lie all about the same small amount above 1 (DUBOIS, 1918 *a*, p. 1416 foot note; 1918 *b*, p. 1328 foot note; 1922 *b*, p. 310; 1923, p. 233). The specific weight of the components of the nervous system lies so little above 1 that, when the ratio of the volumes is taken, instead of that of the weights of these components to the body weight, the exponents are only reduced from 0.27 to 0.2754 and from 0.55 to 0.5508 (DUBOIS, 1920 *b*, p. 623 foot note; 1920 *c*, p. 665 foot note). It appeared that in *Homo sapiens* L. the ratio of the brain weight to the cranial capacity is fairly constant (DUBOIS, 1934 *a*, p. 186). The coefficients of WELCKER for the conversion of the cranial capacity in the brain weight in Man are: 0.94 for cranial capacities between 1500 and 1600 cm^3, 0.93 for cranial capacities between 1400 and 1500 cm^3 (DUBOIS, 1898, p. 428). DUBOIS himself takes somewhat different coefficients in this article. In a later paper (1921, p. 1002 foot note; 1922 *a*, p. 1285 foot note) DUBOIS calculates from CORNEVIN's recorded values 88 % brain weight for capacities of a mean of 650 cm^3, and 93 % brain weight for an average capacity of 100 cm^3 and less, and 91% brain weight for an average capacity of 330 cm^3.

The absolute size of the cerebral capsule

In Dubois' publications we find a number of data about the cranial capacity of Mammalia, which we shall arrange according to size. An asterisk to the generic name indicates that the species concerned also occurs elsewhere in the list.

Funambulus palmarum (L.) 2.3 cm^3 (Dubois, 1939, p. 125);
Sciurus vulgaris L. 6.2 cm^3 (Dubois, 1939, p. 125);
Fennecus zerda (Zimm.) (*Canis zerda*) 19.3 cm^3 (Dubois, 1922 *b*, p. 320 foot note; 1923, p. 242 foot note);
Alouatta seniculus (L.) (*Mycetes seniculus*) ♂ 54 cm^3 (Dubois, 1921, p. 1002; 1922 *a*, p. 1286);
* *Alouatta ursina* (Humb.) (*Mycetes ursinus*) ♀ 54 cm^3 (Dubois, 1921, p. 1002; 1922 *a*, p. 1286);
* *Alouatta ursina* (Humb.) (*Mycetes ursinus*) ♂ 63 cm^3 (Dubois, 1921, p. 1002; 1922 *a*, p. 1286);
† *Mesohippus bairdii* Leidy (Middle Oligocene) 67–70 cm^3 (Dubois, 1930, pp. 264, 265);
Canis lupus L. 161 cm^3 (Dubois, 1922 *b*, p. 320 foot note; 1923, p. 243 foot note; 1922 *c*, p. 317 foot note);
* *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) ♀ 278–341 cm^3 (Dubois, 1921, p. 1001; 1922 *a*, pp. 1284/1285);
Panthera tigris (L.) (*Felis tigris*) ♂ 325 cm^3 (Dubois, 1921, p. 1001; 1922 *a*, pp. 1284/1285);
* *Helarctos malayanus* (Raffl.) (*Ursus malayanus*) ♂ 355–373 cm^3 (Dubois, 1921, p. 1001; 1922 *a*, pp. 1284/1285);
* *Pongo pygmaeus* (Hopp.) ♀ 380–390 cm^3 (Dubois, 1921, pp. 1001, 1003; 1922 *a*, pp. 1284/1285, 1287);
* *Pan troglodytes* (Blumenbach) ♀ 390 cm^3 (Dubois, 1921, p. 1003; 1922 *a*, p. 1287);
* *Pan troglodytes* (Blumenbach) ♂ 420 cm^3 (Dubois, 1921, p. 1003; 1922 *a*, p. 1287);
* *Pan troglodytes* (Blumenbach) 450 cm^3 (Dubois, 1922 *b*, p. 325; 1923, p. 248);
* *Pongo pygmaeus* (Hopp.) ♂ 455 cm^3 (Dubois, 1921, p. 1003; 1922 *a*, p. 1287);
* *Equus caballus* L. dom. Shetland pony 475 cm^3 (Dubois, 1922 *b*, pp. 313/314; 1923, p. 236);
* *Equus caballus* L. dom. light Camargue horse 585 cm^3 (Dubois, 1922 *b*, pp. 313/314; 1923, p. 236);
* *Equus caballus* L. dom. heavy Belgian horse 805 cm^3 (Dubois, 1922 *b*, pp. 313/314; 1923, p. 236);
† *Pithecanthropus erectus* (Dubois) 900–923.5 cm^3 (Dubois, 1922 *b*, p. 325; 1923, p. 248; 1930, pp. 266, 267);
* *Homo sapiens* L. ♀ Australian 1150 cm^3 (Dubois, 1934 *a*, pp. 189, 190);
* *Homo sapiens* L. ♀ average of all European peoples together 1300 cm^3 (Dubois, 1934 *a*, pp. 186, 189);
* *Homo sapiens* L. ♂ Australian 1308–1350 cm^3 (Dubois, 1922 *b*, p. 325; 1923, p. 248; 1934 *a*, pp. 189, 190);
* *Homo sapiens* L. ♂ average of all European peoples together 1450 cm^3 (Dubois, 1934 *a*, pp. 186, 189);

* *Homo sapiens* L. average for upper-german skulls 1484 cm^3 (Dubois, 1898, p. 427);

† *Hydrodamalis gigas* (Zimm.) (*Rhytina Stelleri*) 2125 cm^3 (Dubois, 1897 *a*, p. 4; 1897 *c*, p. 2).

The exact determination of the cranial capacities presents a further difficulty in that a difference is found between the cranial capacity of dried skulls and newly macerated ones (Dubois, 1898, p. 426).

To understand both the absolute size of the cerebral capsule and the relative size of the cerebral capsule with regard to other parts of the skull and to appreciate the position of the cerebral capsule with regard to other functional components of the skull, it is of great importance to know that the cerebral capsule is not an element of the skull with a definite "room of its own" ("Eigenraum") but that the cerebral capsule in part clearly conforms to its surroundings: the cerebral capsule is often more spacious than the brain, which as a matter of fact may conform to the stream-line; in *Lepisosteus* the skull has been so much adapted to the demands of the very elongated shape, that even the brain has been deformed (Van der Klaauw, 1945, pp. 20, 36). Also in Dubois' first publications we find some remarks bearing on this fact. In *Elephas*, where the trunk is highly developed (olfactory organ, organ of touch, organ of capture; is lip, finger, hand and arm), the highly developed trunk muscles attach themselves to the exterior of the "cerebral skull", which exteriorly is very much extended and separated by highly developed diploë and sinuses from the cerebral capsule (see my fig. 1); seemingly, the cerebral capsule too participates in this extension and also the brain itself seems to be extended passively, and the extension of the cerebral surface does not take place by means of folding but by increase of volume (Dubois, 1897 *a*, pp. 14, 39/40; 1897 *b*, pp. 348, 375; 1897 *c*, pp. 8, 27). A passive conforming in the opposite sense, namely the adaptation of the brain to a small skull, is said to occur in *Tachyglossus* (*Echidna*), where the cerebral capsule is smaller than in *Ornithorhynchus*, perhaps due to the much smaller places of attachment for the masticatory muscles (Dubois, 1897 *a*, p. 41; 1897 *b*, p. 376; 1897 *c*, pp. 27/28). After outlining the special demands made by the dentition on the size of the upper jaw – and therefore on the size of the cerebral skull – to procure sufficient room for the attachment of the dentition, Dubois (1898, p. 438) infers from it the reason why in the other Mammalia in contrast with Man the adaptation of the brain to the larger body takes place less by folding of the cortex of the telencephalon than by actual extension of the size. For it would not be an advantage to Man, if the skull were to be considerably enlarged by the extending brain. The dentition of Man, being strongly reduced already, easily finds sufficient place of attachment on the absolutely very large cerebral skull. A large cerebral skull as such is certainly not an advantage; therefore the extension of the surface of the telencephalon in Man and the like is acquired by folding and so an unfavourable extension of the skull is avoided (Dubois, 1897 *a*, p. 13; 1897 *b*, p. 347; 1897 *c*, p. 8; 1898, p. 438).

The relative size of the cerebral capsule

Compared to the so numerous data about the relative size of the brain, those about the cerebral capsule are few in number.

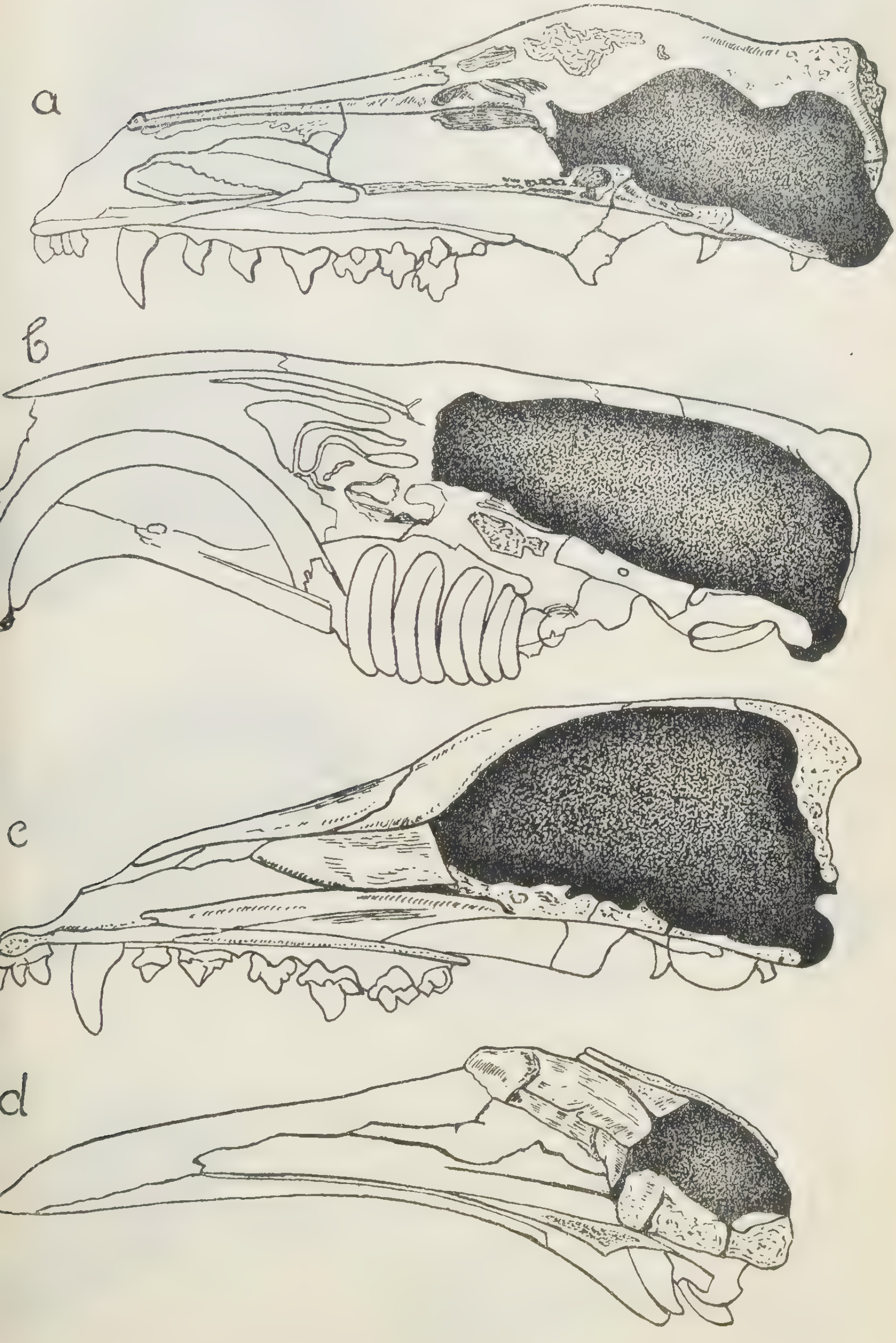
As to the relation between the width of the cerebral cavity and that of the spinal canal, Dubois states the following. According to Marsh in † Dinosauria, the spinal canal, in its whole length, was not seldom wider than the cranial cavity. In † *Stegosaurus* the cross section of the sacral enlargement of the spinal canal was ten times as large as the cranial cavity (Dubois, 1922 *b*, p. 307; 1923, p. 230). In one of the orders of the placental Mammalia from the oldest Eocene, which in general have extremely small cerebral capsules, the cerebral capsule was narrower than the spinal canal, so that it would have been possible to extract the brain through the foramen magnum and the spinal canal (Dubois, 1897 *a*, p. 3; 1897 *b*, p. 337; 1897 *c*, p. 1).

The relative size of the cerebral capsule in proportion to the facial skull is very important to our purpose. Accurate determinations are rare. Stratz (1904, pp. 86, 88, 92) determined the index for the facial and cerebral skull based on their surface in the norma lateralis and found the following values: for *Homo sapiens* L. 42.3, for *Pan troglodytes* (Blumenbach) 90.4, for *Pongo pygmaeus* (Hopp.) 102, for *Equus caballus* L. 450 and for *Gadus aeglefinus* L. 584. In the following pages we shall meet with a number of remarks about the relation of the size of the facial and the cerebral skull. These observations will be preceded by general considerations about the size of the body and of the head, because the latter has great influence not only on the size of the skull, but also on the proportion of cerebral capsule and cerebral skull on the one hand to the facial skull on the other. These observations are of special importance when applied to Mammalia with a large body. We want to discuss three groups separately: the aquatic animals, the terrestrial animals with a small head and a small skull and the terrestrial animals with a large head and a large skull.

In aquatic animals with a large body the considerable upward pressure of the water allows of a large head with a large skull. Indeed, it is very frequent (Cetacea, Pinnipedia, *Hippopotamus*). Neck and legs are short; this restriction of the possibility of fleeing ("Beschränkung der Flüchtigkeit") is possible in this case (STADTMÜLLER, 1936, p. 952); the cerebral skull is small, the facial skull is – also relatively – large (VERSLUYS, 1936, p. 717) (see my figs 2 *d*, *e*, *f* and fig. 3). This fact was established primarily for the secondary aquatic animals, but OWEN already stated for the osseous Pisces (1866 I, p. 92, also p. 249): "The head is larger in proportion to the trunk in fishes than in other vertebrate classes", it contains according to OWEN moreover the gills and the heart.

In most terrestrial animals with a large body the head as well as the skull are small; a light head and skull are important for a life in the air, for the skull has to be carried and smallness is all the more urgent, because a small head goes with a long neck; the latter in its turn is accompanied by long legs which are essential to the animal's possibilities of escape and attack; further, a small, light, mobile head is important for the catching of food (VERSLUYS, 1936, p. 717; STADTMÜLLER, 1936, p. 952). In such cases the absolute measure of the cerebral skull is small and so is the absolute measure of the facial skull, but relatively speaking the facial skull is large (see my figs 2 *a-c*, *g-k*).

In a number of terrestrial animals with a large body, however, we find a large head and a large skull; in this case the neck that has to carry this heavy head is short. The legs are sometimes long, sometimes short; in connection with this the jaws are long (fossil Elephants), unless secondarily a trunk has developed (*Elephas*, *Sus*) (STADTMÜLLER, 1936, p. 952) (see my fig. 1 and fig. 4 *b*). In the former case the facial skull is relatively large, in the latter relatively small. The neck being short, the place of attachment for the neck muscles has to be found on the skull, and consequently the outside surface of the skull and therefore the skull itself is extended (*Elephas* compared with *Giraffa*) (STADTMÜLLER, 1936, p. 952).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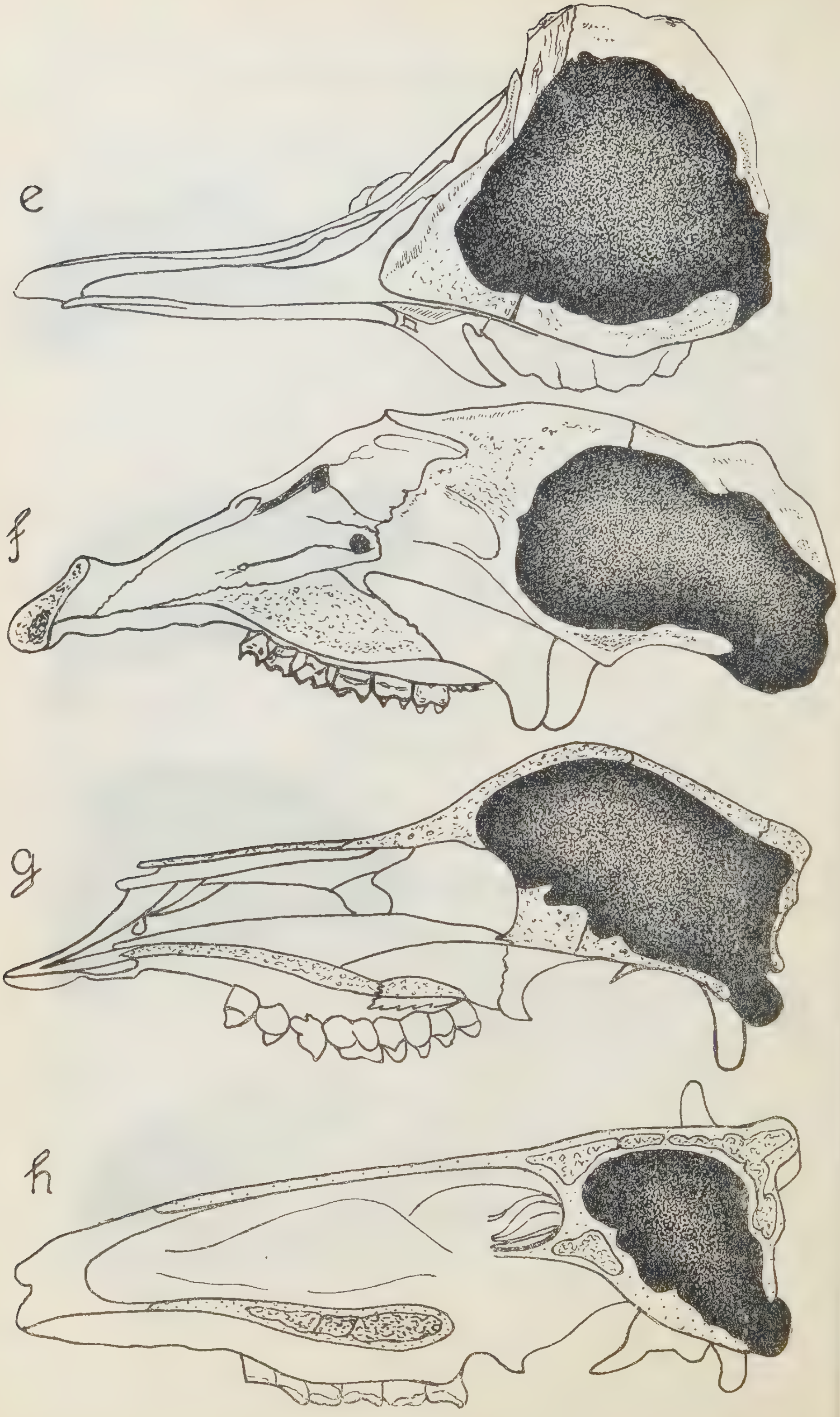
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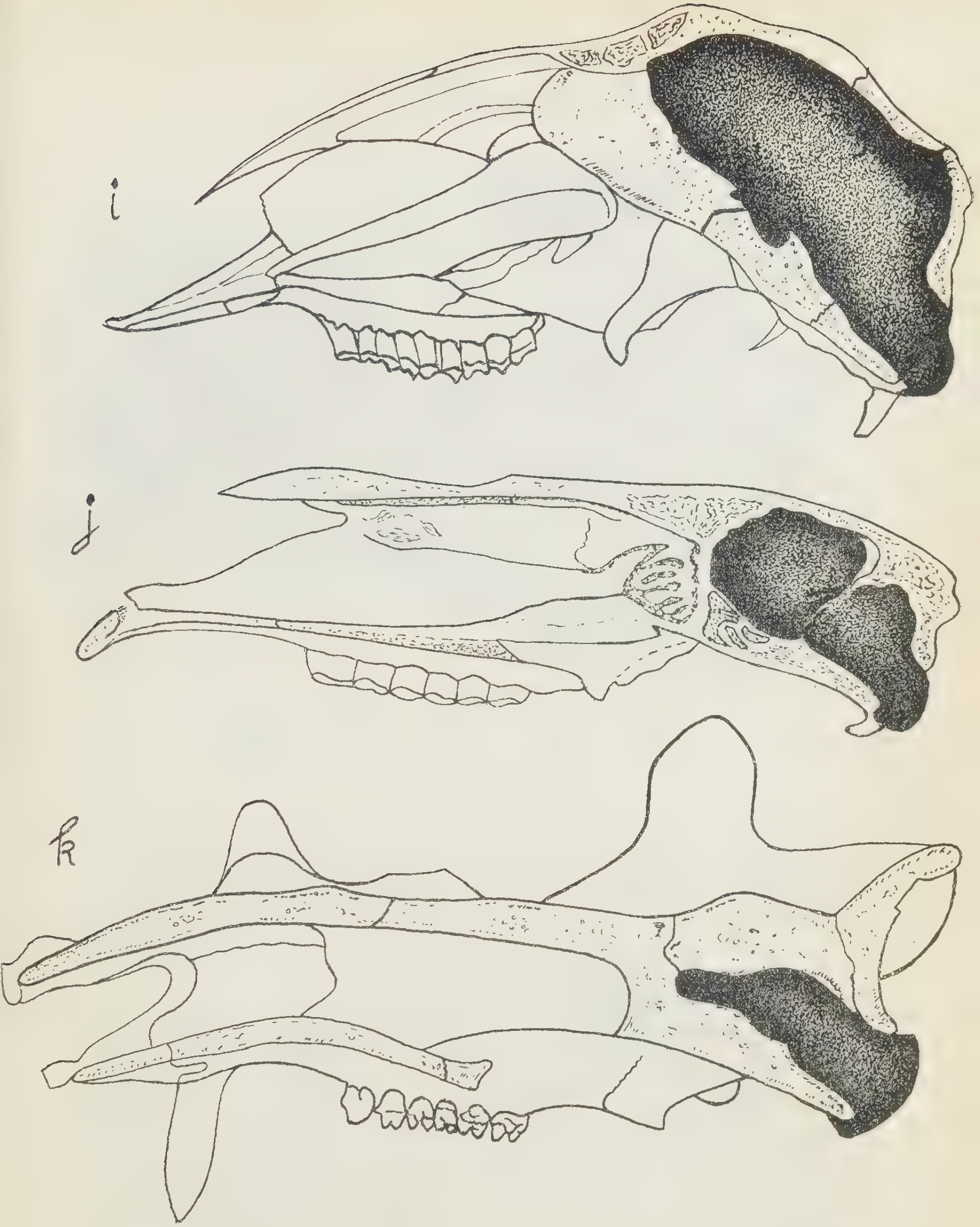

Fig. 2. Right half of Mammal skulls seen from the left side. All skulls are drawn to an equal premaxillon – basion length. *a. Thylacinus cynocephalus* (Harris). After Flower (1885), fig. 70 on p. 236. *b. Castor fiber* L. After Flower & Lydekker (1891), fig. 195 on p. 445. *c. Canis familiaris* L. After Flower & Lydekker (1891), fig. 6 on p. 35. *d. Eubalaena australis* (Desm.). After Flower (1885), fig. 67 on p. 221. *e. Globicephala melaena* (Traill). After Flower (1885), fig. 65 on p. 211. *f. Manatus senegalensis* Desm. After Flower (1885), fig. 68 on p. 224. *g. Cervus elaphus* L. After Bütschli (1910), fig. 174 C on p. 298. *h. Bos taurus* L. dom. After Ellenberger & Baum (1921), fig. 128 on p. 103. *i. Ovis aries* L. After Flower (1885), fig. 62 on p. 193. *j. Equus caballus* L. After Pouchet & Beauregard (1889), fig. 109 on p. 186. *k.* † *Uintatherium mirabile* (Marsh). After Pouchet & Beauregard (1889), fig. 105 on p. 183.

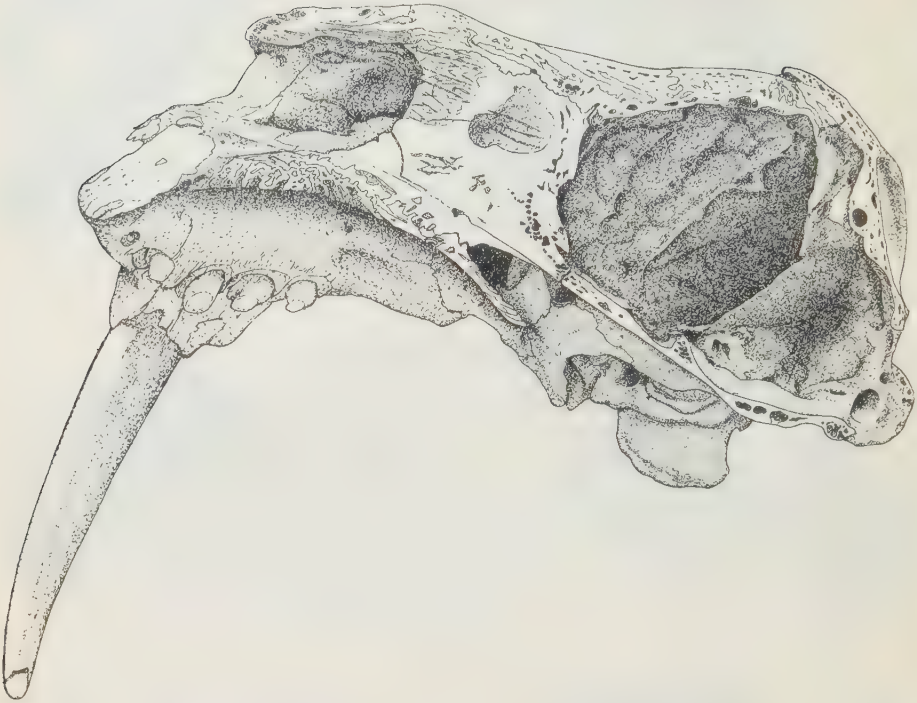

Fig. 3. *Odobenus rosmarus* (L.). Right half of the skull seen from the left side. Coll. Zool. Lab. Amsterdam. 0.37×. Original drawing by B. DE JONG.

The relative size of the cerebral capsule in respect to the weight of the body

Compared with the enormous number of data about the relative size of the brain in respect to the weight of the body, which subject was investigated from every aspect in DUBOIS' life-work, the number of direct data about the size of the cerebral capsule in respect to the size of the body is quite small. But in the case of the Mammalia, where the brain closely conforms to the cavity of the cerebral capsule, we may apply these data to the cerebral capsule. We do not intend to repeat these data here, but shall refer to the above.

In stages of development

When discussing the size of the brain, we saw the reduction of the relative size of the brain in the course of ontogeny and growth. This also holds good for the size of the cerebral capsule in respect to the size of the body. We only want to draw attention to the observation, made by GREGORY (1933, p. 445) that in the larval stages of many Teleostei the brain case is large and swollen. In proportion to the facial skull, the cerebral capsule as well as the cerebral skull are relatively more and more reduced in the course of ontogeny and growth (see my figs 4 and 5). We only want to point out the humanlike character of the skull, of the facial skull especially, of youthful Anthropoid Apes.

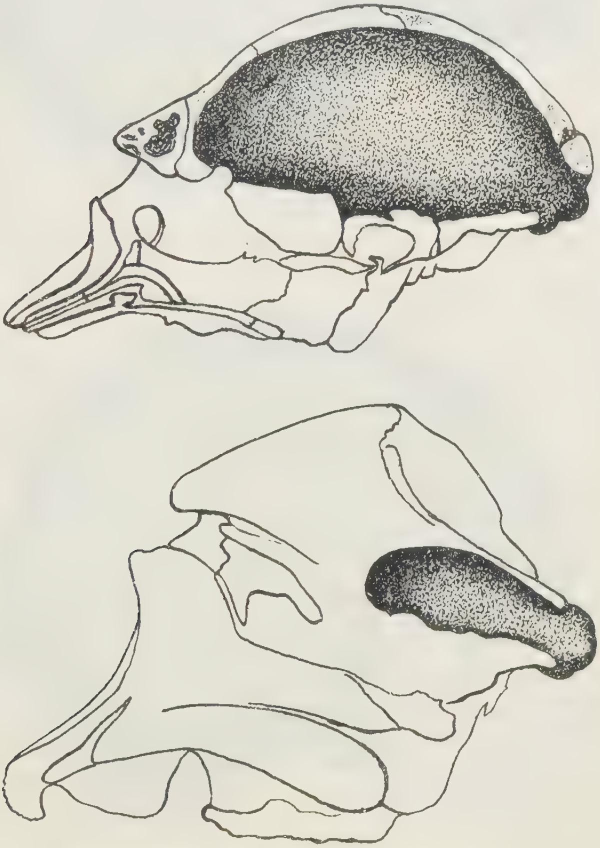

Fig. 4. *a. Loxodonta africana* (Blumenbach) (*Elephas africanus*). New-born. Right half of the skull seen from the left side. 0.25×. After FLOWER (1885), fig. 63 on p. 205. *b. Loxodonta africana* (Blumenbach) (*Elephas africanus*). Adult. Right half of the skull seen from the left side. 0.08×. After FLOWER (1885), fig. 64 on p. 205.

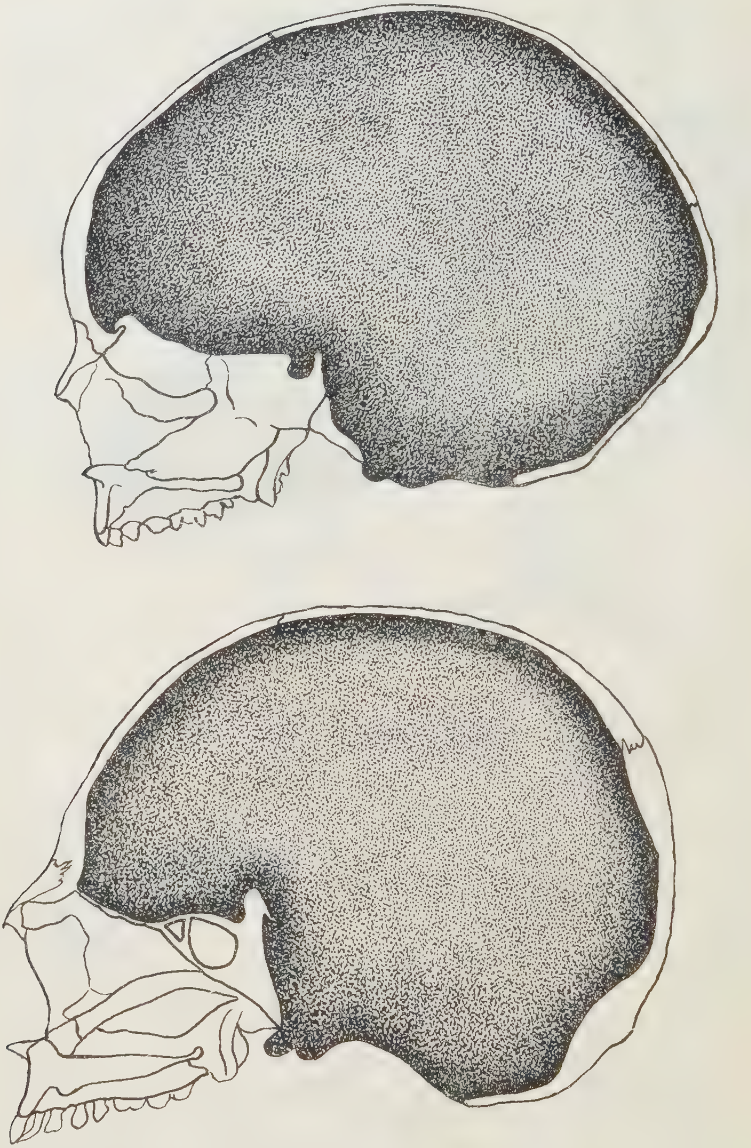

Fig. 5. *a. Homo sapiens* L. New-born. Right half of the skull seen from the left side. 0.50×. After FLOWER (1885), fig. 53 on p. 151. *b. Homo sapiens* L. Adult. Left half of the skull seen from the right side in mirror image. After VON BARDELEBEN (1896–1909) I, fig. 49 on p. 226.

In adult animals

Though the number of data about the cerebral capsule in relation to the size of the body is very small compared with that about the weight of the brain in relation to the body weight, yet we want to retain the same classification of the data.

In both sexes

In the list of data about the absolute size of the cerebral capsule, we already saw that in *Homo sapiens* L. this size diverges. The same applies to the relative size in relation to the weight of the body. Also among the Anthropoidea sexual differences may be considerable.

In various individuals of the same species

Concerning *Homo sapiens* L. and the Anthropoidea, it is again a well-known fact, that the individual variability of the size of the cerebral capsule may be considerable, and therefore perhaps the relation of the size of the cerebral capsule to the body weight may also be variable.

Very curious and important is the condition in various large specimens (races?) of *Canis familiaris* L. In very small specimens the so-called pug-headed skulls occur; they develop when with the reduction of the size of the body the cerebral skull decreases less in size than the facial skull (Owen, 1866 II, p. 504; Stadtmüller, 1936, p. 951) (see my fig. 6).

In different races

The cranial capacity of the male Australian is 8.4 % lower than that of the male European, which can be considered as a real racial difference (Dubois, 1934 *a*, p. 191). In the Eskimo the average cranial capacity is highest of all existing peoples, whereas the Negroes show a relatively lower cranial capacity (Dubois, 1934 *a*, p. 192). We saw in the above that, although the real coefficient of cephalisation may be the same for all recent human races, yet it allows of a different specific size of the brain. In the same way the specific size of the cranial capsule perhaps may be different too.

Previously, we pointed to the fact, that small individuals of a domesticated species have comparatively more, large individuals comparatively less brain than related wild species of corresponding mean body weight. The same also applies to the proportional size of both cerebral capsule and cerebral skull. Dubois (1930, pp. 254, 255) refers in this connection to the relation in size of the cerebral skull of a "toy-terrier" ("Zwergpinscher") and of a *Fennecus zerda* (Zimm.) (*Canis zerda*) (see my figs 6 and 7).

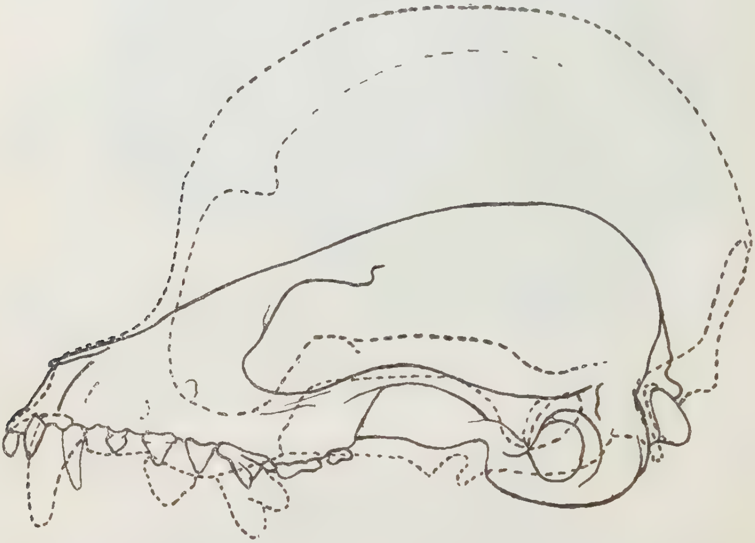

Fig. 6. *Fennecus zerda* (Zimm.). Skull seen from the left side. After Dubois (1930), fig. 1. *Canis familiaris* L. dom. (Pekingese). Skull seen from the left side. After Dubois (1930), fig. 2. Both skulls are drawn to the same premaxillon-basion length and are combined in one drawing.

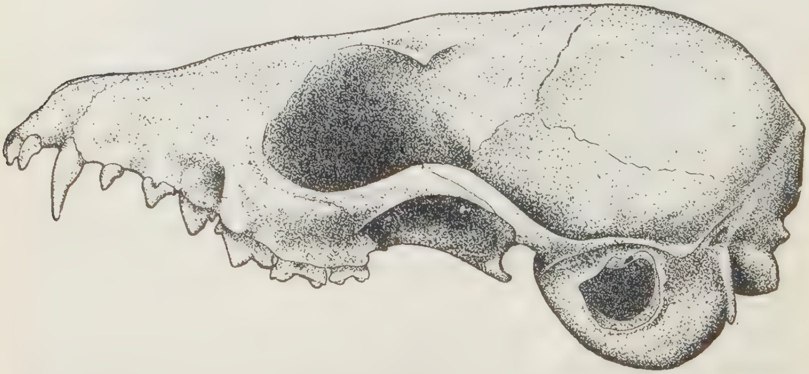

Fig. 7. *Fennecus zerda* (Zimm.) ♂. Skull seen from the left side. R.M.N.H. Leiden, No. 1248. R.D. 31-7-'23. 1.20×. Original drawing by dr C. de Jong.

In homoneuric animal species

Direct data about the relative size of the cerebral capsule in proportion to the body weight are lacking, but they can be easily derived from the data about the proportion of brain weight and body weight in homoneuric species of animals, which we mentioned above. The fact that when homoneury obtains the small species have a relatively large brain, means that the cerebral capsule is also relatively large, whereas in large species not only the brain will be relatively small, but the cerebral capsule as well (see my fig. 8). When the body increases in size the facial skull will not participate in the relative reduction of the cerebral capsule.

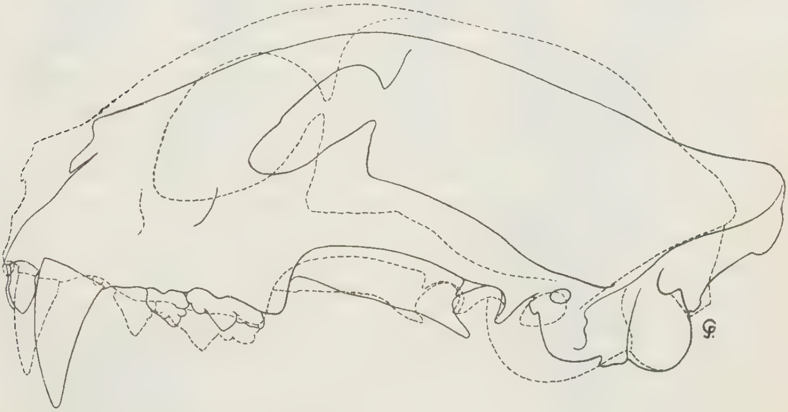

Fig. 8. *Panthera tigris* (L.) and *Felis catus* L. Skull seen from the left side. Both skulls are drawn to the same premaxillon-basion length and are combined in one drawing. Original drawing by dr C. DE JONG.

Such species have a relatively larger facial skull than the small, related homoneuric species, relative in respect of the cerebral capsule, and this generally means also in respect of the cerebral skull. But in a number of cases the cerebral skull has been (outside measurement) strongly extended owing to the development of spongy parts, sinuses, cristae, ridges, *etc.*

In heteroneuric animal species

Compared with the very extensive body of facts about the relation between brain weight and body weight in heteroneuric species of animals, which is at our disposal thanks to the elaborate investigations about the cephalisation by Dubois, we have very few direct data about the relation between cranial capacity and size of the body. Nevertheless a few things may be derived from the data about the brain throwing a light on the cerebral capsule.

We may assume that, when the body weight is the same among related animals or in any case among animals having the same morphological plan, the species with a higher value of the coefficient of cephalisation will have a larger cerebral capsule as well as a relatively smaller facial skull. In the species of animals mentioned as examples for comparison, however, the body weight in most cases is not the same and neither is the coefficient of cephalisation (see my fig. 2). Besides, given an equal body weight, the best examples would be those of animal species belonging to one and the same phylogenetic series. This too, is rarely if ever the case. We may deem ourselves happy, if – and this was often the case when Dubois set up the terms of a geometrical progression – the animal species concerned belong to one and the same family or order, in which the coefficient of cephalisation is for a certainty known to be strongly divergent. Now we know of a number of very old fossil groups that their coefficient of cephalisation was very low, lower than that of related recent species of animals. Such cases are very suitable for our purpose.

In the earliest forms of Reptilia, from the Mesozoicum, though for the rest very differentiated and often gigantic, the encephalon, especially the telencephalon, that means in my opinion the cerebral capsule, possesses an extremely slight volume (Dubois, 1922 *b*, p. 307; 1923, p. 230; 1930, p. 247). Dubois adds that they in this respect are differing from forms immediately following them and from modern forms (see my figs 9-12). We saw, however, that this is sometimes denied for the Reptilia. In the † Pelycosauria on the other hand the cerebral capsule is said to be very much larger in proportion to the very small and short cerebral capsule of the † Cotylosauria; this is connected with the increase of the brain in the † Pelycosauria (Versluys, 1936, pp. 774, 801). The brain – meant is in my opinion the cranial cavity – remains insignificant in † *Triceratops* and † *Stegosaurus* as in † *Diplodocus*, it remains small in the † Pterosauria (Dubois, 1924 *a*, p. 326; 1924 *b*, p. 437). Besides in the † Pterosauria also in the † Theromorpha the cranial cavity is very small (Dubois, 1922 *b*, p. 307; 1923, p. 230). In † *Diplodocus* with a body length of 24 meters the cranial cavity is only 9 cm long and 5 cm wide, whereas that

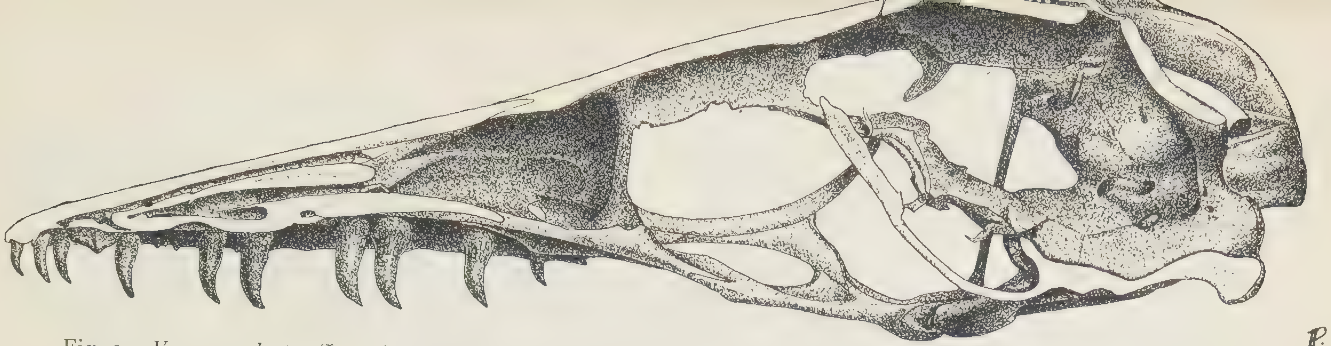

Fig. 9. *Varanus salvator* (Laur.) ♀. Right half of the skull seen from the left side. R.M.N.H. Leiden, Reg. no. 7051. Sumatra/China? 1.68×. Original drawing by L. P. Pouderoyen.

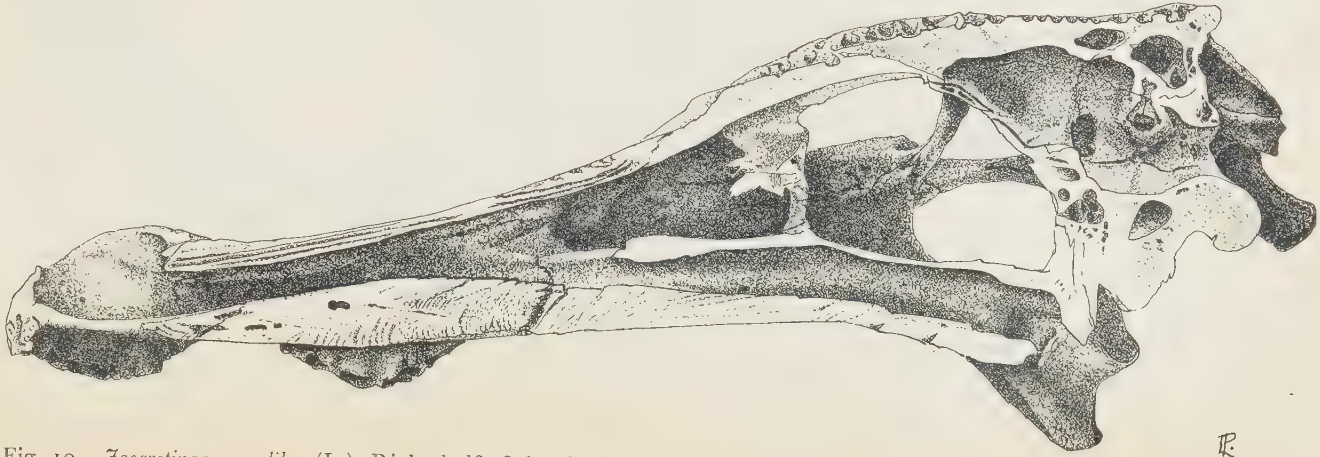

Fig. 10. *Jacaretinga crocodilus* (L.). Right half of the skull seen from the left side. R. M. N. H. Leiden, Cat. ost. C. 0.75×. Original drawing by L. P. Pouderoyen. -

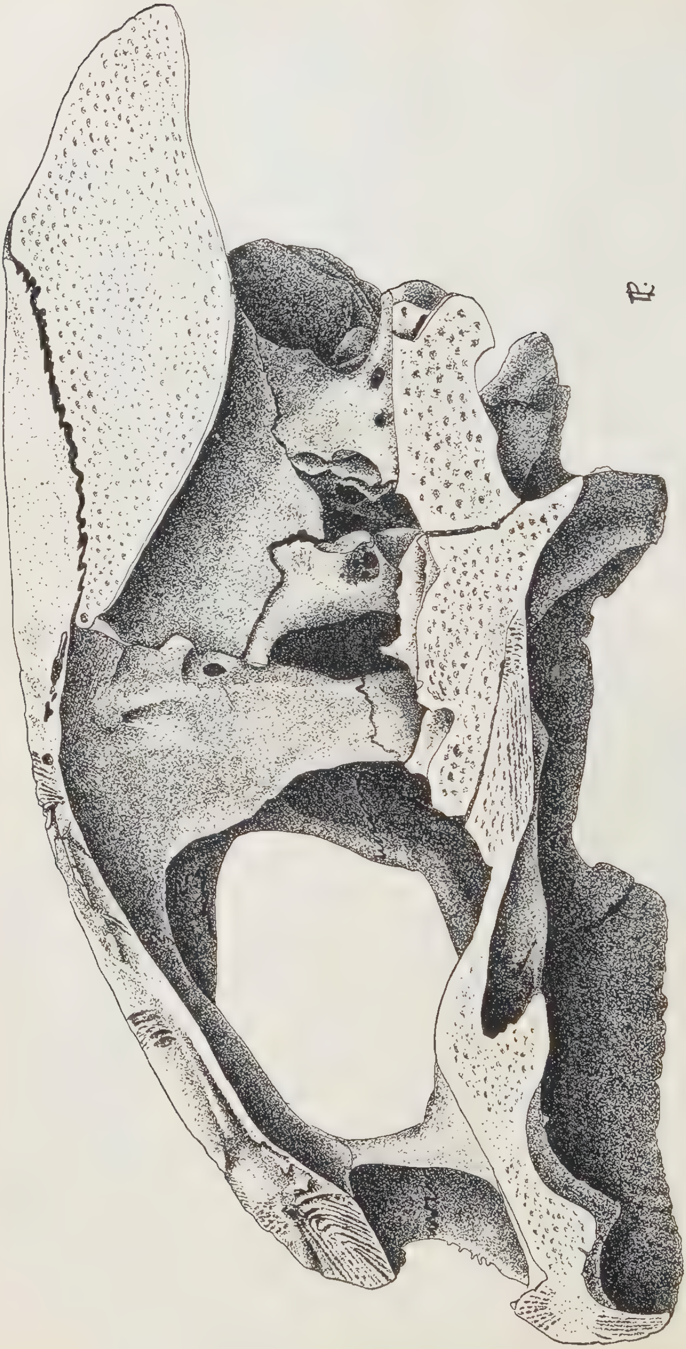

Fig. 11. *Chelonia.* Left half of the skull seen from the right side in mirror image. Coll. Zool. Lab. Leiden. 0.78×. Original drawing by L. P. POUDEROYEN.

of an adult Alligator, with a tenth of that maximum body length of † *Diplodocus*, has a length of 6½ cm and a width of 3 cm (DUBOIS, 1922 *b*, p. 307; 1923, p. 230).

In the earliest forms of Aves as well the encephalon, that means in my opinion the cerebral capsule, possesses an extremely slight volume, in this respect differing from the forms immediately following them and from the modern forms (DUBOIS, 1922 *b*, p. 307; 1923, p. 230) (see my figs 13-15). According to MARSH † *Ichthyornis* possessed only the third of the cranial cavity of *Sterna sandvicensis* Lath. (*Sterna cantiaca*), with which it shows a considerable resemblance in size (DUBOIS, 1922 *b*, p. 307; 1923, p. 230). In the anatomical series † *Euparkeria capensis* Broom (one of the † Pseudosuchia of the Trias), † *Archaeornis siemensii* (Dames), *Columba livia* (L.) dom. (see my fig. 14) the brain – meant is in my opinion the cerebral capsule – becomes larger and larger and the brain in the recent Aves may be called large (BÖKER, 1937, p. 89). OWEN (1866 II, p. 61) already observed concerning the cranial cavity for the brain "that of the smallest Humming-bird is proportionally greater than in any other animal, while that of the great *Dinornis* is almost crocodilian in its contracted area".

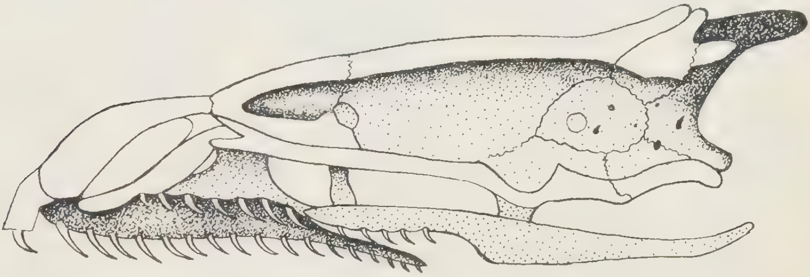

Fig. 12. *Python*. Right half of the skull seen from the left side. After BÜTSCHLI (1910), fig. 158 B on p. 275.

In the earliest forms of Mammalia as well, the encephalon, that means the cerebral capsule in my opinion, possesses an extremely slight volume, in this respect differing from the forms immediately following them and from modern forms (DUBOIS, 1922 *b*, p. 307; 1923, p. 230) (see my fig. 2). In many Eocene Mammalia the brain and especially the telencephalon was absurdly small and remained at a low stage of organisation (DUBOIS, 1924 *a*, p. 326; 1924 *b*, p. 437; 1930, p. 247). In the Miocene, partly

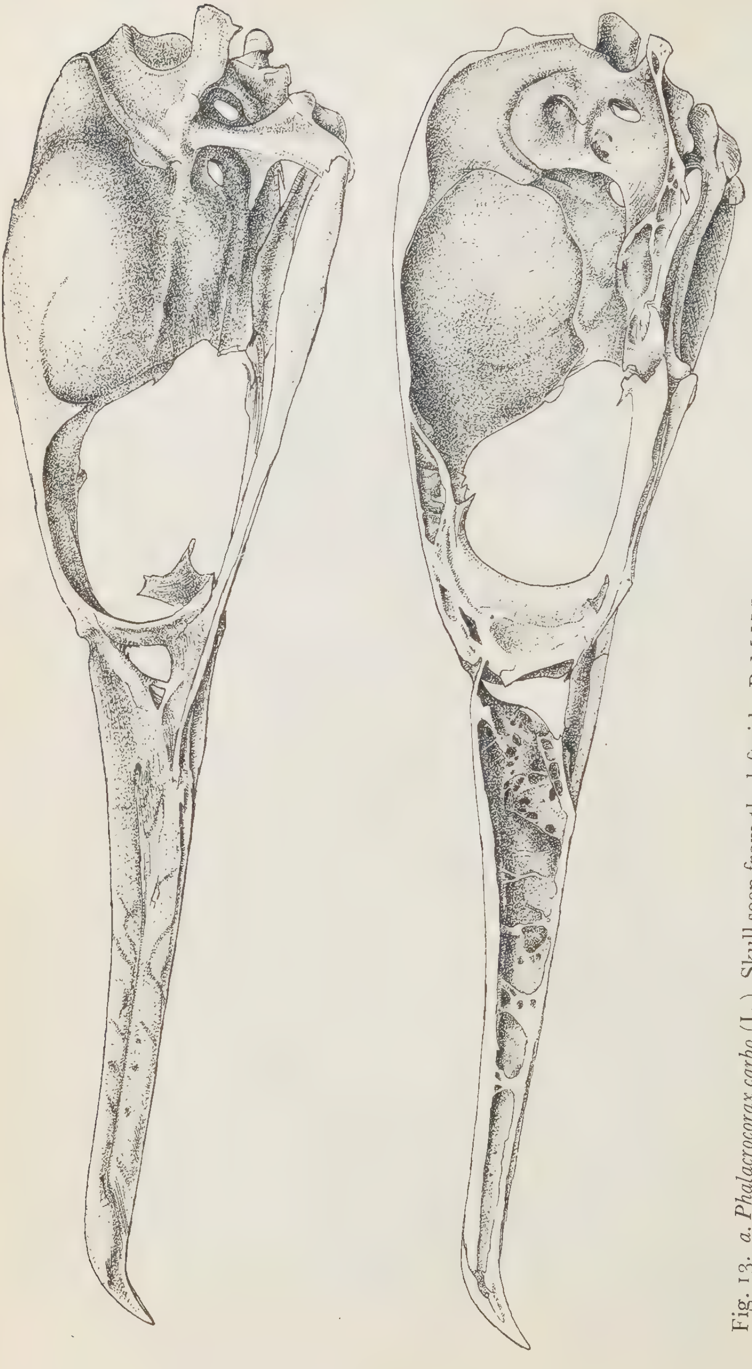

Fig. 13. a. *Phalacrocorax carbo* (L.). Skull seen from the left side. R.M.N.H. Leiden. 1.40×. Original drawing by P. van ’t Zelfde. b. *Phalacrocorax carbo* (L.). Right half of the skull seen from the left side. R.M.N.H. Leiden. 1.40×. Original drawing by P. van ’t Zelfde.

already in the Eocene Period, the brain, that means in my opinion the cerebral capsule, in the Mammalia reaches the volume of most modern types (Dubois, 1922 *b*, p. 308; 1923, p. 231). † Creodontia possessed a very small encephalon (that means the cerebral capsule), as the comparison of the skull of † *Arctocyon* with a specimen of *Canis* of a similar body size shows (Dubois, 1922 *b*, p. 307; 1923, p. 230). The † Condylarthra had also brains of extremely small volume, as the comparison of the skull of † *Phenacodus* with that of a Pig of similar size of the body shows (Dubois, 1922 *b*, pp. 307/308; 1923, pp. 230/231). The

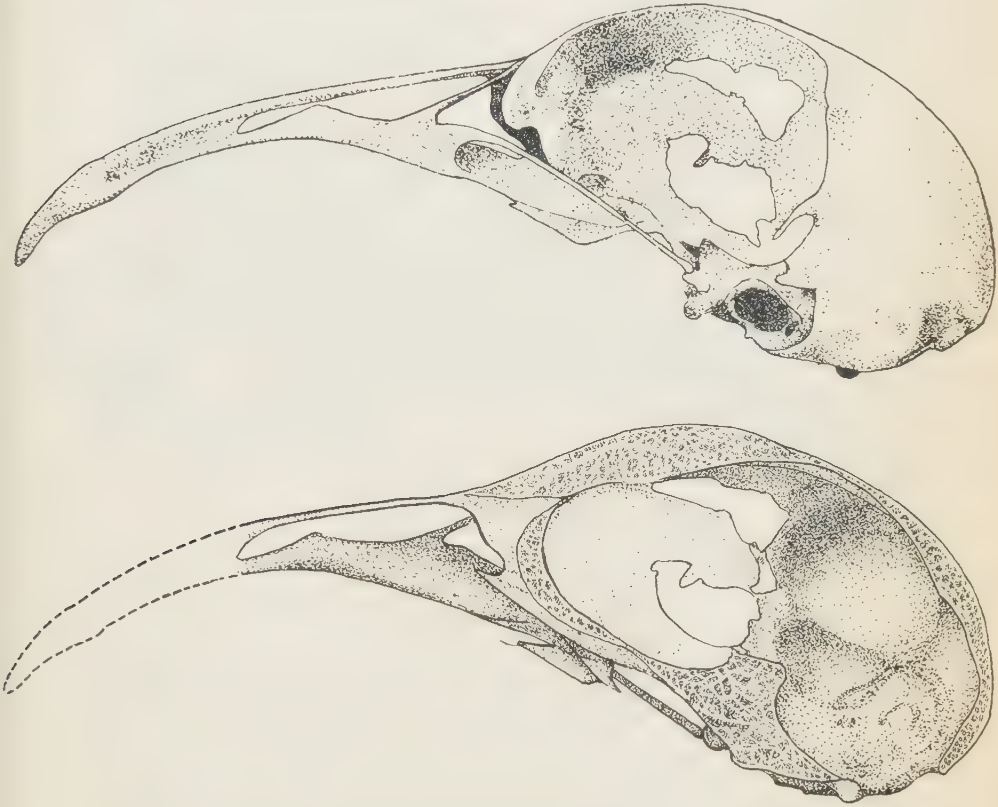

Fig. 14. *a. Columba livia* L. Skull seen from the left side. Zool. Lab. Leiden, No. 4387. 2.4×. Original drawing by G. van Gelderen. *b. Columba livia* L. Right half of the skull seen from the left side. Zool. Lab. Leiden, No. 4387. 2.4×. Original drawing by G. van Gelderen.

† Amblypoda had very small brains, that means very small cerebral capsules in my opinion, as the comparison of the skull of † *Coryphodon* with that of a *Rhinoceros* of similar size shows (Dubois, 1922 *b*, p. 308; 1923, p. 231; see also Stadtmüller, 1936, pp. 950, 956, 981).

There are also some striking examples of related species of animals, of which the body weight is not too divergent, whereas the cephalisation is very different indeed. Thus the volume of the brain - meant is in my opinion the cerebral capsule – in † *Pithecanthropus* is small in comparison with Man, large in comparison with the Anthropoid Apes (Dubois, 1934 *b*, p. 74). This influences as well the relation between cerebral skull and facial skull. A process, to be compared with the development of a pug-headed skull in small canine races, is also found among the Anthropoidea and Man, but here it is especially due to an absolute as well as a relative extension of the brain (Stadtmüller, 1936, p. 951).

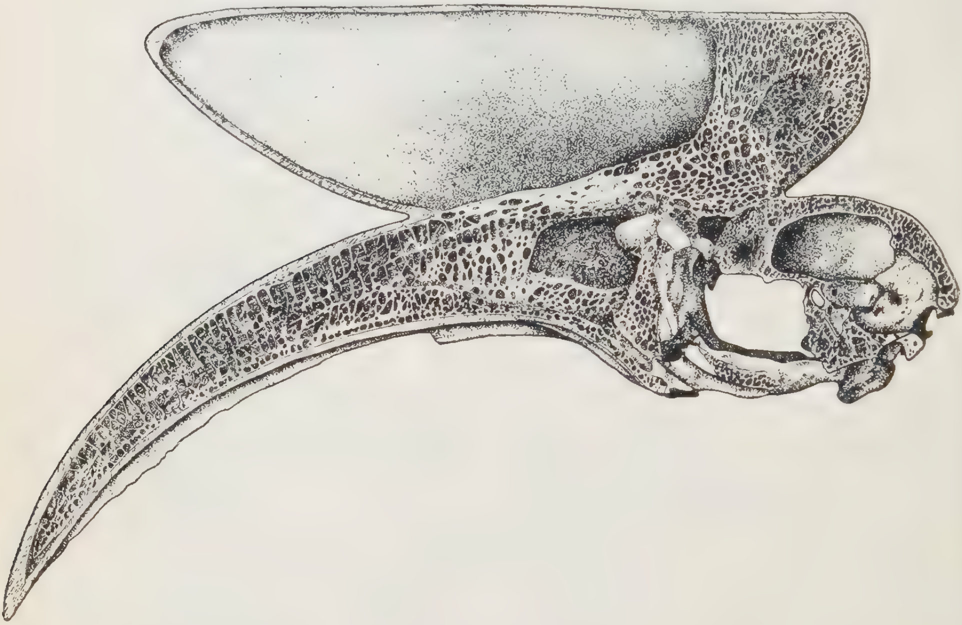

Fig. 15. *Buceros rhinoceros sylvestris* Vieill. Right half of the skull seen from the left side. R.M.N.H. Leiden, Cat. C. Java 1828. 0.52×. Original drawing by G. van Gelderen.

There are, however, also data about the proportion of cerebral skull to facial skull in recent animal species that differ in body size and cephalisation, and even are not directly related (see my figs 2 and 16). It stands to reason that these data are of little general significance and of no significance at all for the understanding of this subject without further analysis of the relation between the body weight and the value of the coefficient of cephalisation. Among other things this applies to the following cases. In the Marsupialia (see my fig. 2 *a*) the absolute and the relative size of the cerebral skull are small, also compared to those of the Monotremata (OWEN, 1866 II, p. 335; STADTMÜLLER, 1936, pp. 950/951, 964, 966). That in the Platyrhina "the cranium is proportionally larger and the jaws less, as the species are smaller in size" (OWEN, 1866 II, p. 529) is not obviously a matter of course, because both body weight and the coefficient of cephalisation are so strongly divergent. In a sense the same holds good for the observation made by OWEN (1866 II, p. 525) that the cerebral skull in *Daubentonia* (*Chiromys*) is large in relation to the facial skull, as compared with lower Mammalia of similar size, when we do not know what is understood by lower Mammalia. The same is the case with the observation made by KINGSLEY (1925, p. 219), that in the lowest Primates the cerebral skull in its relation to the facial skull is as small as in the Carnivora (see my figs 2 *c*, 7 and 8).

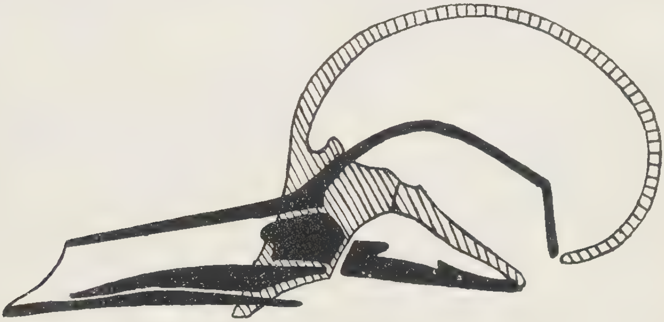

Fig. 16. *Cervus* and *Homo*. Right half of the skull seen from the left side. Combined figure. After BÜTSCHLI (1910), fig. 171 on p. 294.

In a number of cases the relation of the coefficients of cephalisation as well as that of the body weights is known; in such cases, provided that both these factors work in the same direction, the difference in the relation between facial skull and cerebral skull is easily understood. In the above we concluded from the value for the index of facial to cerebral skull given by STRATZ, that this index is much higher for *Equus caballus* L. than for *Homo sapiens* L. and for Anthropoid Apes, which is easily understood considering the fact that the value of the coefficient of cephalisation of *Equus caballus* L. is lower, whereas its body weight is higher. We may add, that also STADTMÜLLER (1936, p. 981) mentions *Equus caballus* L. as the most striking example of the predomination of the facial part over the cerebral part among the Mammalia or at any rate among the Mesaxonia (see my fig. 2 *j*).

We may also add, that a ♂ specimen of *Panthera tigris* (L.) possessed the same cranial capacity of 325 cm^3 as a ♀ specimen of *Helarctos malayanus* (Raffl.); here the effect of the lower cephalisation of *Panthera* (4th stage) was compensated by that of the body weight which was probably four or six times higher (DUBOIS, 1921, p. 1001; 1922 *a*, pp. 1284/1285). That a specimen of *Helarctos malayanus* (Raffl.) may have the same cranial capacity as a specimen of *Pongo pygmaeus* (Hopp.) is understandable when the body weight is the same, because they belong to the same stage of cephalisation (DUBOÍS, 1921, p. 1001; 1922 *a*, pp. 1284/1285).

Neither does a comparison of animal species from various classes of the Vertebrata or, if desired, a mutual comparison of those classes themselves appear quite suitable in principle for general conclusions, because both the value of the coefficient of cephalisation and the body weight are divergent. Still, it may be maintained in general that in the series of the Vertebrata we see from class to class a distinct increase of the size of the cerebral capsule and consequently of the cerebral skull. Consequently in this series the cerebral skull generally speaking becomes larger in proportion to the facial skull.

In the Pisces the size of the brain case is small (see my figs 27, 43 and 50). Compared to other Pisces in Euselachii the brain case is relatively large (see my fig. 17). GREGORY (1933) stated for *Zeus* that the brain case is small (p. 271, fig. 148). The relatively small size of the brain case is also to be read from the illustrations given by GREGORY (1933). I only want to mention here the illustrations of the skulls with sagittal section of the brain case; these are: the † Cephalaspidae (fig. 2 C), the † Pa-

laeoniscidae (fig. 14 B), *Chlamydoselachus* (fig. 14 A), *Tarpon atlanticus* (C. & V.) (fig. 32 A), *Salmo* sp. (fig. 46, 47 B) (see my fig. 18), *Roccus lineatus* (Bl.) (fig. 1, 119 A, 119 B) (see my fig. 19), *Lagocephalus laevigatus* (L.) (fig. 168) and *Thunnus* (fig. 191 B).

In the Amphibia the size of the brain case is small (see my fig. 20, also my fig. 38). The same is the case in the Reptilia (see my figs 9–12, also my fig. 44).

A relatively distinctly larger cerebral capsule and cerebral skull is found in the † Theromorpha (VERSLUYS, 1936, pp. 719, 741), Aves (see my figs 13, 14, also my figs 34 and 52) and Mammalia (see my fig. 2, and also my figs 1, 3-8, 16, 26, 35, 37, 46 and 48), where the strongly developed brain has such a marked influence on the form of the skull. The considerable ontogenetic start that the brain has of the development of the skull, is kept up in these higher Vertebrata and is expressed in the aforesaid great influence on the structure of the skull (HALLER VON HALLERSTEIN, 1934, p. 191; MARINELLI, 1936, p. 809; VERSLUYS, 1936, pp. 719, 741). In some cases the cerebral capsule is relatively small, as, *e.g.*, in *Buceros* (see my fig. 15).

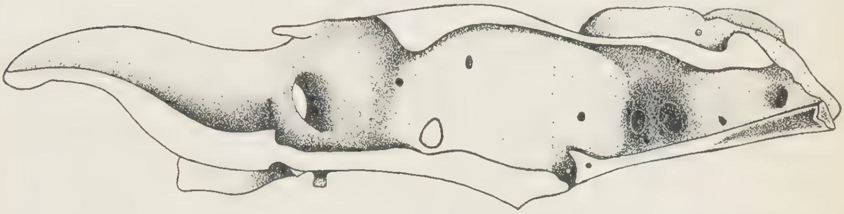

Fig. 17. *Squalus acanthias* L. Right half of the skull seen from the left side. Nat. size. Original drawing by C. L. VAN HELDEN.

We will give two examples here that may almost be taken as extremes. OWEN (1866 I, p. 146; 1866 II, p. 571) states for the Loricata (Crocodilia) that the brain case is "miserably small" and that the main part or the brain case proper "may be filled by a man's thumb in a skull of three feet in length" (see my fig. 10). On the other hand we have Man, of whom CUVIER (quoted by STRATZ, 1904, p. 85) said: "L'homme est celui de tous les animaux qui a le crâne le plus grand et la face la plus petite" (see my fig. 5).

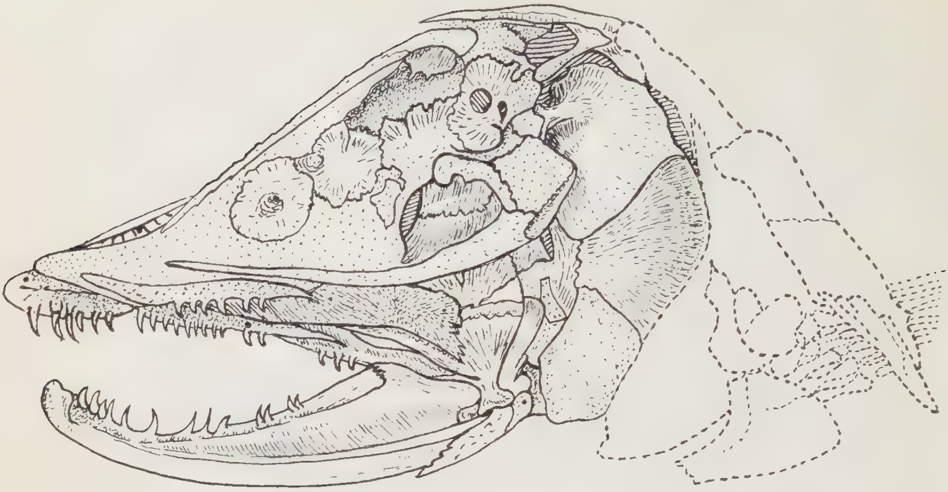

Fig. 18. *Salmo.* Right half of the skull seen from the left side. After GREGORY (1933), fig. 46 on p. 152 and fig. 47 B on p. 153 (combined).

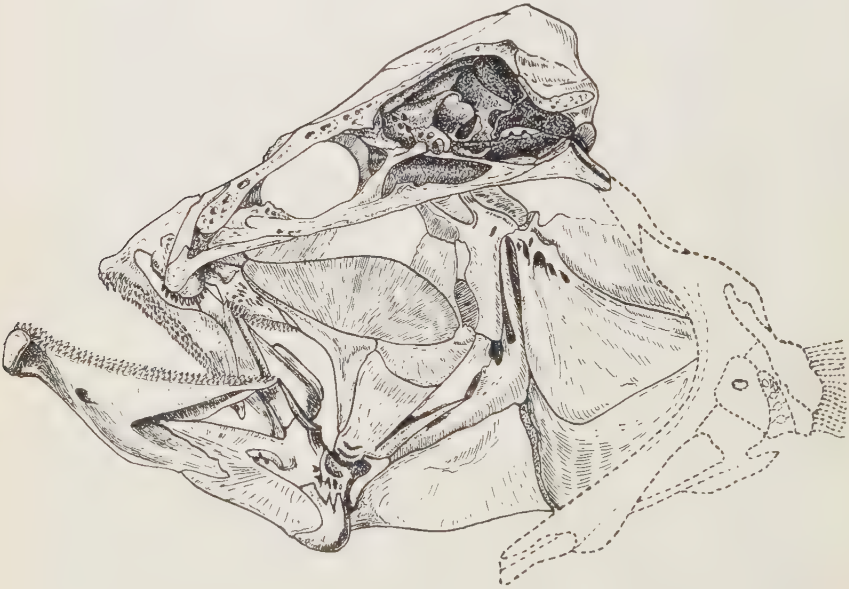

Fig. 19. *Roccus lineatus* (Bl.). Right half of the skull seen from the left side. After GREGORY (1933), fig. 119 A and B on p. 245 (combined).

f. The shape of the cerebral capsule

Among the skulls of the Teleostei GREGORY (1933, p. 431) distinguishes three types. In the first type, the high type, in which we find a dominance toward height, the occiput deepens vertically but not as fast as the back, so that the skull roof slopes upward to the apex; forward growth of the snout naturally tends to lower the slope of the skull roof (fig. 291 E, 290 C). In the second type, the long type, in which we find a dominance toward length, the occiput remains low; forward growth of the snout has a similar effect. In the third type, the broad type, in which we find a dominance toward width, the head is wide and low and no doubt also the brain case in the broad neurocranium. Thus we find, according to GREGORY (1933, fig. 293), a divergence of the primitive Percoid (*e.g.*, *Lates*, see my fig. 21) into very wide (*e.g.*, *Myoxocephalus*, see my fig. 22 and *Ogcocephalus*, see my fig. 23) and very high types (*e.g.*, *Pomacanthus*, see my fig. 24 and *Chaetodipterus*, see my fig. 25).

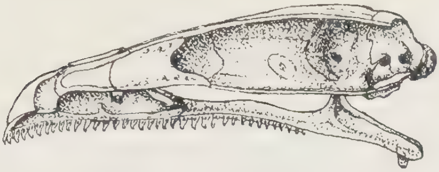

Fig. 20. *Rana esculenta* L. Right half of the skull seen from the left side. 2.0 × . Original drawing by C. F. A. BRUYNING.

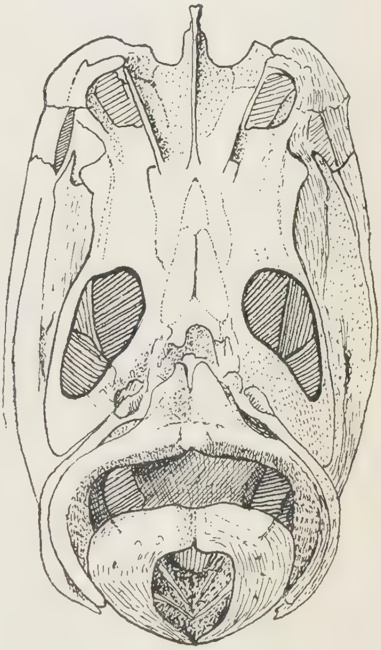

Fig. 21. *Lates*. Skull seen in front view. After GREGORY (1933), fig. 293 A on p. 429.

In *Capros aper* (L.) the cranial vault is very short antero-posteriorly and rises steeply in front into a very high sagittal crest (p. 273, fig. 149 A).

In *Symbranchus*, in which all the vertical diameters are reduced, the brain case appears like a long, gently tapering tube in side view (p. 352). The top view of the skull of *Zoarces anguillaris* (Peck) shows the relative length and narrowness of the brain case (p. 375, fig. 254 B). In *Anarhichas* the brain case in the top view is narrow, in part at least due to the powerful development of the jaw muscles (p. 377, fig. 254 C). In *Tylosurus* the brain case is a rather narrow stiff trough (p. 221).

In *Alabes* the brain case is widened due to the telescoping of the snout (p. 352). In *Astroscopus* the brain case is excessively short and wide (p. 368). In *Pelor japonicum* C. & V. the cranial vault is considerably widened and shortened in connection with the fact that the eyes are turned upward and pushed backward, which is in its turn connected with the slope of the upper jaw (GREGORY, 1933, p. 438, fig. 206).

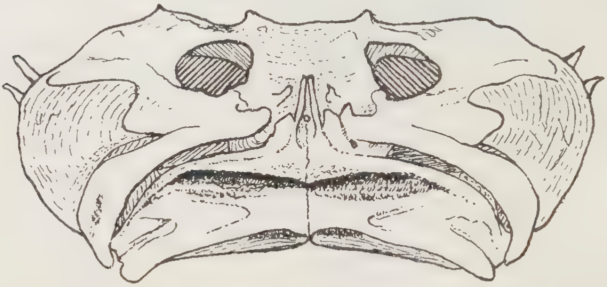

Fig. 22. *Myoxocephalus*. Skull seen in front view. After GREGORY (1933), fig. 293 C on p. 429.

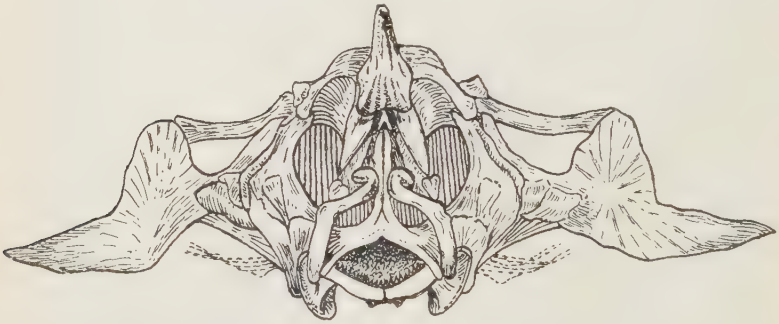

Fig. 23. *Ogcocephalus*. Skull seen in front view. After GREGORY (1933), fig. 270 on p. 398.

The proportionately broader brain which, as we have seen, occurs in large animals, in a higher cephalised brain, in case of strongly developed olfactory organs, of large caudally placed eyes and in animals with a rapid and nimble ("gewandte") locomotion, will entail in the higher Vertebrata, where the brain fills up the cerebral capsule, a proportionately more brachycephalic skull.

In the serpent *Bitis* the cerebral skull is relatively very broad and short, which is indeed connected with the caudal extension of the very long quadratum (VERSLUYS, 1936, p. 785, fig. 604).

A distinct platycephaly with a comparatively small capacity of the upper part of the skull is found in skulls of Apes, also in † *Homo neanderthalensis* King, causing the lower half of the cerebral capsule to lie deeper. This platycephaly in † *Homo neanderthalensis* King was not determined, at least not chiefly, by the comparatively small size and low stage of development of the encephalon, but by external mechanic factors, chiefly in connection with the position and poise of the skull on the spinal column, just as the platycephaly in *Hylobates* (*Symphalangus*) *syndactylus* (Desm.), in contrast to the other Hylobatids, can only be explained by its comparatively large jaws (DUBOIS, 1921, pp. 990, 994; 1922 *a*, pp. 1274, 1277). When comparing the skull of the small *Funambulus palmarum* (L.) with that of the larger *Sciurus vulgaris* L. and with the gigantic *Ratufa* it appears that contrary to expectation the brain case of the small animal was strikingly low-vaulted. The cranial low-vaultedness in *Funambulus palmarum* (L.) may be a consequence of the fact that in this

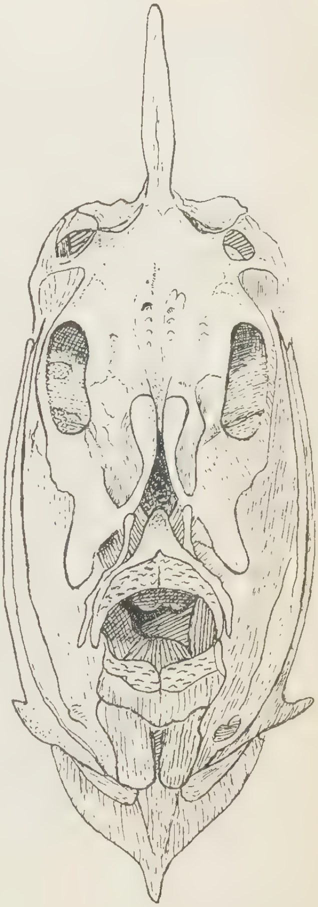

Fig. 24. *Pomacanthus*. Skull seen in front view. After GREGORY (1933), fig. 293 B on p. 429.

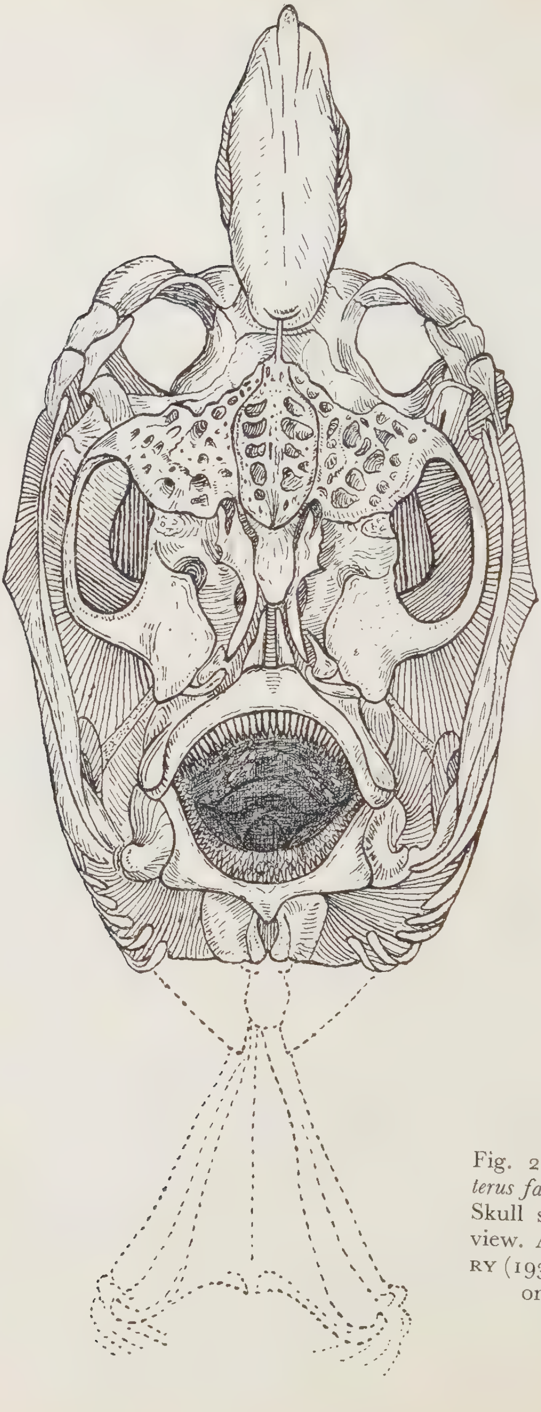

Fig. 25. *Chaetodipterus faber* (Brouss.). Skull seen in front view. After GREGORY (1933), fig. 152 B on p. 276.

species the skull is much more oblong than in *Sciurus vulgaris* L. (Dubois, 1939, p. 125). In the † Ichthyosauria the cerebral skull is short and high (Versluys, 1936, p. 797).

g. The position

We will not discuss here the situation of the cerebral capsule with respect to the surrounding functional components of the skull. When we deal with these surrounding elements their situation with respect to the cerebral capsule will be mentioned.

Still, we want to point out here the situation of the brain case, which is connected with the situation of the basis cranii. Marinelli (1929, pp. 131, 132) points out, that in the Cavicornia the basis cranii does not only lie in the elongation of the cervical part of the vertebral column, but that also the insertion of the horns on the skull is in line and level with the basis cranii; this causes in those Cavicornia, which carry their heads high, the steep slanting of the brain case ("welche den Kopf erhoben tragen, die steile Aufrichtung der Hirnkapsel") (see my figs 2 *h* and *i*). In *Equus caballus* L., on the other hand, the basis cranii does not rise to the frontal wall, but runs almost parallel, so that the cerebral capsule is not slanting upwards (see my fig. 2 *j*).

h. Homology and non-homology

When judging of the size and the difference in size of the cranial cavities for the brain, we should bear in mind, that these cavities of the skull are not strictly homologous in the different groups. In the higher groups, that is, in the Aves, but especially in the Mammalia, the cavity for the brain is wider (Stadtmüller, 1936, pp. 847/848, 909/910), first because not only the roof of the primordial neurocranium has disappeared for the greater part and the secondary cranial roof has developed outside it, but because the latter is extended and is vaulted; secondly, because the original lateral wall and the caudal wall – and in the Primates also the plane of the fenestrae olfactoriae – of the primordial neurocranium have rotated downward, in the higher Mammalia to such an extent even, that the bottom of the cranial cavity is convex (Stadtmüller, 1936, p.954). Another cause of the extension of the cavity for the brain in the skull in higher groups is that certain originally extracranial regions have been included into the cavity for the brain; we may mention here: the cavity of the neocranium; the spatium s. cavum epiptericum, the spatium supratrochleare and the spatium supracribrosum of the Mammalia; the "trigemino-facialis-chamber" of ALLIS; in the Ophidia and Testudinata the space added owing to the development of a new lateral wall in the orbitotemporal region, formed by bony plates ventrally growing down from the roof and in the † Anomodontia the space inside the epipterygoid, which has been incorporated into the wall of the cavity for the brain.

We may conclude by pointing out, that the bony lining of the cavity for the brain may give an incorrect appreciation of the size of the cerebral capsule, in the cases that the cerebral capsule is incompletely ossified. In the Sauropsida with a tropidobasic kinetic skull, for instance, the bony partition of the cerebral capsule in the orbitotemporal region is incomplete.

2. SKELETAL LABYRINTH

a. Introduction

By the skeletal labyrinth we understand the cavity in the skull, containing the membranaceous labyrinth, together with the thin layer of cartilage or bone, lining this cavity. This layer of bone is sometimes extremely hard and is then called bony labyrinth; in this case it is generally embedded in a spongy bone mass, as in Aves and less clearly in many Mammalia, except the Cetacea with their very compact petrosa (DE BURLET, 1934, p. 1296).

Here too we may try to deduce data about the size of the skeletal labyrinth from data about the size of the membranaceous labyrinth.

b. The connection between the size of the skeletal labyrinth and the size of the membranaceous labyrinth

In the Marsipobranchii (Cyclostomata) there is only a narrow space, filled with connective tissue, between the membranaceous and the cartilaginous labyrinth (DE BURLET, 1934, p. 1333). In the Reptilia the skeletal labyrinth is not so closely conform with the membranaceous labyrinth as is the case in the Mammalia (VERSLUYS, 1936, p. 758). Consequently the sizes of the membranaceous and the skeletal labyrinths may also be somewhat more different from each other.

In Pisces the skeletal labyrinth has often very incompletely developed, especially on the median side; this is extremely so in *Hippocampus* (DE BURLET, 1934, pp. 1333, 1382). In such cases the size of the membranaceous labyrinth in this direction, does not define the size of the skeletal labyrinth.

c. The size of the membranaceous labyrinth

The absolute size of the membranaceous labyrinth

Generally there is no connection between the size of the body and the size of the membranaceous labyrinth (DE BURLET, 1934, p. 1321).

In Pisces we find the largest absolute sizes of the membranaceous labyrinth. Especially the canales semicirculares can attain a great length in Selachii: in *Somniosus microcephalus* (Bl. Schn.) *(Laemargus borealis)* 18.5 cm (DE BURLET, 1934, p. 1321). This, however, does not give any clue as to the absolute size of the membranaceous labyrinth as a whole, because there are very great differences among the Vertebrata in the relative size relations of sacculus, lagena and canales semicirculares, as a comparison of the situation in *Gobius niger* L., *Cyclopterus lumpus* L. and Cetacea shows (DE BURLET, 1934, pp. 1294, 1310, 1311, 1321). That part of the membranaceous labyrinth, containing the sagitta or main otolith, is also very large in those cases where this otolith is very large (GREGORY, 1933, p. 440).

In determining the absolute size of the membranaceous labyrinth one should know whether or not to include the saccus endolymphaticus. For this saccus can be very large; in *Gekko* an offshoot even enters the orbita (DE BURLET, 1934, p. 1331).

The relative size of the membranaceous labyrinth

Generally there is no connection between the size of the membranaceous labyrinth and the size of the body (DE BURLET, 1934, p. 1321).

In determining the relative size of the membranaceous labyrinth it is of the utmost importance to take the age of the animal into consideration. For the membranaceous labyrinth does not or hardly grow after birth, as has been proven by investigations in *Homo* and in *Cavia* (DE BURLET, 1934, pp. 1321/1322).

d. The shape of the membranaceous labyrinth

We saw above that there may be much diversity as to the form of the membranaceous labyrinth in various Vertebrata, owing to the mutual difference in the size of the parts. Consequently taking a measure in one single direction is insufficient for the determination of the size of the membranaceous labyrinth.

e. The size of the skeletal labyrinth

The absolute size of the labyrinth

I have not seen any data about the absolute size of the skeletal labyrinth [1]. We may conclude from the above that in certain Pisces the skeletal labyrinth will also be large.

The relative size of the skeletal labyrinth

In various groups of Pisces the labyrinth is so strongly developed, comparatively speaking, that the strong, sometimes very strong broadening of the regio otica of the skull has to be attributed entirely or for the greater part to this fact. HOLMGREN & STENSIÖ (1936, pp. 329, 373, 401) state this emphatically for the † Placodermi, the Crossopterygii, *Neoceratodus* and the † Palaeoniscidae (see also GREGORY, 1933, p. 440).

In Amphibia the volume of the labyrinth has decreased in comparison to that in Pisces (STADTMÜLLER, 1936, p. 616).

The cavity of the skeletal labyrinth, as well as the cavity of the membranaceous labyrinth, is relatively essentially larger in the Reptilia than in the Mammalia (VERSLUYS, 1936, p. 758).

Consequently, according to KINGSLEY (1925, p. 192), the otic capsules in the Mammalia are relatively smaller than in other groups.

The relative size of the skeletal labyrinth may appear from the following ratio between the volume of the ear capsules and the volume of the cerebral capsule, which is for *Rana* 1 : 4, *Lacerta* 1 : 10, *Lepus* 1 : 20, *Homo* 1 : 70 (VOIT, cited by STADTMÜLLER, 1936, p. 870).

f. The shape of the skeletal labyrinth

In this connection we may refer to our above statements about the form of the membranaceous labyrinth, as well as to our statements about the incomplete development of the median wall of the skeletal labyrinth, which also influences the size of the skeletal labyrinth.

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[1] For the absolute size of the bony labyrinth in a number of adult Mammalia see: J. A. KEEN (1942), Trans. roy. Soc. S. Africa **29**, pp. 49-57. (Postwar addition in the manuscript)

g. The position

The skeletal labyrinth lies in the wall of the cerebral skull, which is thickened on this spot. The skeletal labyrinth lies outside the cerebral capsule, as this only comprises the innermost bone layer of the cerebral skull.

In the lower Vertebrata up to and including the Reptilia, the ear capsules lie in the lateral wall of the skull (KINGSLEY, 1925, p. 136; STADTMÜLLER, 1936, p. 915).

In Aves – especially in species with a downward deflection in the base of the skull ("geknickt") (MARINELLI, 1936, p. 814) – and in Mammalia (GAUPP, 1916, p. 91; KINGSLEY, 1925, p. 192; STADTMÜLLER, 1936, p. 876) the lateral wall of the primordial neurocranium with the otic capsules is tilted sidewards and aborally and has thus broadened the basis of the primordial neurocranium, so that the ear capsules lie in the floor of the cranial cavity. The fact that the otic capsules in the Mammalia do not lie clearly in the side wall, is also connected with the small size of the ear capsules in the Mammalia (STADTMÜLLER, 1936, p. 871). Nevertheless, in the lowest Mammalia and as a matter of fact also in some higher Mammalia the otic capsules are found to stand more or less in an upright position, the canales semicirculares lying dorsally of the pars cochlearis and the ear capsules forming an important part of the lateral wall of the skull (STADTMÜLLER, 1936, p. 868).

There is also a connection between the position of the canales semicirculares of the membranaceous labyrinth in the position when at rest of the head and the incline of the axis of the earth. The remaining part of the membranaceous labyrinth and the skeletal labyrinth as well, is also influenced by this in its incline and position. Thus, the otic capsule of the higher Mammalia has rotated, compared with its position in Reptilia (STADTMÜLLER, 1936, p. 870). However, also within a certain systematic group we find differences in the position and incline of the labyrinth in connection with the differences in the incline of the head. Thus we find in *Homo*, in connection with the erect carriage a rotation backwards and downwards of the os petrosum

(Stadtmüller, 1936, p. 952). So the position of the skeletal labyrinth shows a certain degree of independence with regard to the axes of the cerebral capsule.

A further difference in the position is due to the fact that the pars cochlearis in the higher Vertebrata extends secondarily into the basal plate. This is the case in Mammalia (Gaupp, 1916, pp. 67, 91; Stadtmüller, 1936, pp. 840, 850, 868, 915), in Aves (Marinelli, 1936, p. 814) and in Loricata (Crocodilia) (Versluys, 1936, p. 759; *n.b.* Kingsley, 1925, p. 136 mentions for Reptilia in general: "the lagenar part of the ear extending into it").

In Aves the canalis semicircularis anterior possibly extends into the tectum synoticum (Marinelli, 1936, p. 815).

h. Homology and non-homology

The above mentioned differences in size and position cannot be explained by assuming that the labyrinths compared should be non-homologous. In the Vertebrata they are mutually homologous.

3. ORBITA

a. Introduction

By the orbita we understand here that cavity of the skull which contains the eye ball and part of its auxiliary organs, together with the skeletal wall of this cavity. This skeletal wall is only the thin bone layer, closely joining and only partly covering the eye ball. Viewing the skull on the surface the orbita can be surveyed in full, so that no thickenings and the like of covering skeleton parts give a wrong impression of the size of the orbita.

Exact data about the size of the orbita itself are few in number, but rather many exact data about the size of the eye ball itself are available. In using them for our purpose it is indispensable, however, to know the relation between the size of the eye ball and the size of the orbita.

b. The connection between the size of the orbita and the size of the eye ball

About this relation we may mention the following[1]).

In *Lampetra fluviatilis* (L.) (*Petromyzon fluviatilis*) the eye is surrounded by a globular capsule of connective tissue and embedded in a large venous sinus, traversed by the eye muscles; in other words, the eye is much smaller than the cartilaginous orbita, which is otherwise very little developed, because there is little cartilage in the orbita (FRANZ, 1934, pp. 998, 1001). In Elasmobranchii (Plagiostomi) we meet with great differences in the depth of the orbita; in those forms, where there is ample space between the eye ball and the wall of the skull, this space is filled by a padding tissue; amongst others this is found in the Hypotremata (FRANZ, 1934, p. 1019). In *Chimaera* the orbita is almost completely filled by the large eye (FRANZ, 1934, p. 1017). In *Polypterus* the orbita is far too large for the eye, which occupies it for a small part only (HOLMGREN & STENSIÖ, 1936, p. 388). In *Astroscopus y-graecum* (C.V.) according to GREGORY (1933, pp. 369, 439) the eye is large, but the orbita small (see my figs 42 and 50); as these data are given in different places, I do not know if we may draw from them any conclusion about a very close fitting of the eye into the orbita.

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[1]) For the relation between the size of the orbita and of the eye in Primates see: A. H. Schultz (1940), Amer. J. phys. Anthrop. **26**, pp. 389-408. (Postwar addition in the manuscript)

In *Apteryx* the conspicuously small eye lies in a large spacious ("geräumige") orbita (FRANZ, 1934, p. 1128) (see my fig. 57). In Aves, the orbita is generally not very spacious ("geräumig"). In *Phalacrocorax* (see my fig. 13) and apparently also in *Eudyptes* with its very mobile eyes, the orbita is filled by the eye to a lesser degree than is otherwise the case; here it may be a case of convergence in these two much-diving birds (FRANZ, 1934, p. 1199).

The very small eyes of *Talpa europaea* L. do not fill the normally developed orbitae; these orbitae principally contain connective tissue and fat (FRANZ, 1934, p. 1258). The rudimentary eye of *Spalax typhlus* Pall., which has only the size of a hempseed ("hanfkorngross"), also lies in a large orbita (FRANZ, 1934, p. 1262).

The loss of the eye in *Homo* is accompanied by a diminution of the orbita (RAUBER-KOPSCH, 1922, p. 119; 1940, p. 230).

Apart from these direct data about the relation between the size of the orbita and the size of the eye ball, there are also a number of indirect data, which can be deduced from the development of eye muscles and eye glands and from the telescope- and tubus-eyes.

The eye muscles lie in the orbita. Now there is a certain proportionality between the strength of the eye muscles and the development of the eye. It seems that in Mammalia the inverse proportionality between the strength of the eye muscles and the relative size of the eye may be found as well as this direct proportionality, which exists from Selachii upwards. In Elasmobranchii (Plagiostomi) in a narrow orbital space ("knappe Orbitalraum"), the thickness of the eye muscles is lessened and *vice versa* (FRANZ, 1934, pp. 1019, 1253, 1262). By no means therefore are we able to find a measure for the size of the orbita by adding a certain percentage of the size of the eye ball to the volume of the eye ball.

Where and in how far one or more of the eye glands lie in the skeletal orbita, cannot be ascertained with any accuracy from the data in literature. In the Loricata (Crocodilia) the lacrymal gland lies against the roof of the orbita ("unter dem Dache der Augenhöhle") (FRANZ, 1934, p. 1194). In the Salientia (Anura) after the metamorphosis, the voluminous gland of HARDER penetrates into the interior of the "soft orbita", between the eye muscles (FRANZ, 1934, p. 1092). The name "Orbitaldrüse" (glandula orbitalis), which is the name of the homologon of HARDER's gland in the Apoda (Gymnophiona), where this gland is exorbitantly large in proportion to the reduced very small eyes, might also point to its being situated in the orbita (FRANZ, 1934, pp. 1085, 1092, 1093).

The same relation between a very large HARDER's gland and small reduced eyes is found in Sauria (Lacertilia) with reduced eyes and in Serpentes (Ophidia); at least, in the latter, the very large HARDER's gland extends far backwards over the ventral side of the eye ball (FRANZ, 1934, pp. 1093, 1106, 1106/1107, 1191, 1193).

In *Eudyptes crestatus* (J. F. Miller) (*Eudyptes chrysocome*) the 25 mm long HARDER's gland (the eye is also 25 mm in section) lies on the bottom of the orbita ("auf der unteren Seite der Orbita"), with which no doubt the soft orbita will be meant (FRANZ, 1934, p. 1198). As the skeletal orbita often lacks a bottom, these data do not mean that the skeletal orbita contains ventrally so much space under the eye ball.

In Rodentia with eyes turned very much sidewards, the very large eye gland is situated on the nasal side, whereas the temporal gland is small; the reverse is to a high degree the case in Primates with their eyes focused forward (FRANZ, 1934, p. 1278). This situation has been compared to that, caused by lack of space in the orbita, which makes itself felt in the development of eye muscles and sclera of deepsea fishes and Striges (Franz, 1934, pp. 1262, 1278). From this it cannot be concluded with any certainty, however, whether and in how far these eye glands lie in the skeletal orbita in Rodentia and Primates. On the other hand, the eye glands of *Notoryctes typhlops* Stirling, the very small eyes of which are said to be "enclosed" by the powerful eye glands ("mächtige Augendrüsen") (Franz, 1934, p. 1257) do probably lie in the skeletal orbita for the greater part.

Also the telescope-eyes in certain deepsea fishes and the tubus-eyes in eagles and Striges (see my fig. 34) can, to my mind, teach us something about the relation between the size of the eye ball and the size of the orbita. The telescope-eyes of the deepsea fishes are mostly found in species with small bodies and large eyes, whereas in Aves species with small bodies and relatively large eyes seem not so apt to develop telescope-eyes. The view that telescope-eyes and tubus-eyes are not lengthened eyes, but narrowed eyes in the sense that relatively the peripheral parts are lacking, may mean, in my opinion, that the eye ball with this circumference fits into the orbita, in other words, that this circumference of the eye ball is a measure for the size of the orbita, at least of the border of the orbita (Franz, 1934, pp. 1028/1029, 1130/1131; Böker, 1937, pp. 17, 20).

The contrary, in a sense anyhow, occurs where the eyes taper strongly conically and bulge considerably out of the orbita. Here, the length of the main axis of the eye ball is no measure for the depth of the orbita. This phenomenon is met with in all eyes to a greater or less extent. It is to a high degree the case in *Anableps tetrophthalmus* Bl. (see my fig. 40), with its water- and air-eye, half of which is emerging ("halb herausragend"), according to Franz (1934, p. 1051). As an extreme case of this phenomenon are to be considered the longstemmed eyes of the postembryonal *Stylophthalmus* and the shorter stemmed eyes of some other species of fish larvae (Franz, 1934, pp. 1050,1061). In these the eyes in these stages of development will undoubtedly not fit at all into the skeletal orbita.

c. The size of the eye ball

The absolute size of the eye ball

When in literature more than one measure of the size of the eye ball is given, I have always taken the rostro-caudal horizontal diameter in the following; and for this reason, that very often the skeletal orbita is lacking a clear ventral wall, whereas a front wall and a back wall are generally present.

When in literature only one measure is given for the diameter, this is not quite accurate, because the diameters of the eye ball are not exactly the same in every direction. The rostro-caudal horizontal diameter is often largest, because a certain horizontal ellipticity ("Horizontalelliptizität") of the bulbus exists. In no class of the Vertebrata it is quite absent, but, in Sauria(Lacertilia), Aves and Mammalia it is stronger than in *Rana*, but less than in Pisces, at least in Selachii (FRANZ, 1934, pp. 1009, 1021, 1065, 1129, 1203).

The following absolute measures of the size of the bulbus oculi are for the greater part taken from FRANZ (1934). I have arranged the data, within each class of the Vertebrata in order of increasing value.

FRANZ states for the eye ball of Pisces (1934, pp. 998, 1007-1009, 1019, 1025, 1026, 1051-1056, 1059, 1060, 1063, 1064):

Ipnops murrayi Günther 0 mm; the only Vertebrate with the eye completely absent;
Troglichthys rosae (Eigenmann) 0.04–0.12 mm;
Typhlichthys subterraneus Girard 0.16 mm;
Amblyopsis spelaeus Dekay max. 0.2 mm, often less;
Myxine glutinosa L. hardly ("knapp") 0.5 mm;
Cyclothone ca 0.5 mm;
Cetomimus 0.7 mm;
Chologaster agassizii Putnam 0.7 mm (smallest eyes of this genus);
Chologaster papilliferus Forbes 1 mm;
Bdellostoma polytrema Girard (*Bdellostoma dombey*) 1 mm;
Hippocampus 1–3.5 mm;
Gonostoma 1.3 mm;
Chologaster cornutus Agassiz 1.4 mm (largest eyes of this genus);
Protopterus 2 mm;
Mordacia lapicida (Rich.) 3 mm;
Syngnathus phlegon Risso 3–4 mm;
Lampetra fluviatilis (L.) (*Petromyzon fluviatilis*) 4.9 mm;
Muraena anguilla L. (*Anguilla vulgaris*) 5 mm;
Ostracion 8 mm;
Lepidosiren 10 mm;
Squalus (*Acanthias*), *Mustelus* and *Galeorhinus* (*Galeus*) 15–25 mm;
Scyliorhinus (*Scyllium*) 16 mm;
Etmopterus (*Spinax*) 17.5 mm;
Lepisosteus 19.5 mm;
Acipenser sturio L. 24 mm;
Eulamia (*Carcharias*) 35 mm;

Chimaera 35 mm;
Mola mola (L.) (*Orthagoriscus mola*) 37 mm;
Isurus nasus (Bonnaterre) (*Lamna cornubica*) 45 mm;
Cetorhinus maximus (Gunner) (*Selache maxima*) 63 mm.

Concerning the Amphibia Dubois (1919 *a*, p. 505; 1919 *b*, p. 713) and Franz (1934, pp. 1065, 1083, 1085, 1086) give the following measurements:

Ichthyophis glutinosus (L.) 0.6 mm; indeed, in Apoda (Gymnophiona) generally (vide too Böker, 1937, p. 9) the eyes are very small; among them genera are found with the most rudimentary eyes in the Vertebrata, apart from *Ipnops*;
Proteus max. 1.2 mm under the influence of light;
Typhlotriton larvae 1.3 mm;
Hyla arborea (L.) 4.6 mm;
Rana temporaria L. 5.8 mm (according to Dubois in "*Rana fusca*" 6.6 mm).

For the eyes of Reptilia Dubois (1913, p. 598; 1914 *a*, p. 652; 1919 *a*, p. 505; 1919 *b*, p. 713) and Franz (1934, pp. 1096-1097, 1102, 1105-1107, 1116, 1117, 1120) give the following measures:

Voeltzkowia mira Bttgr. ca 0.3 mm;
Typhlops 0.4 mm;
Cadea blanoides Stejn. (*Amphisbaena punctata*) 1.2 mm;
Anguis fragilis L. 2.8 mm;
Lacerta agilis L. 3.2 mm;
Hemidactylus 3.7 mm;
Hemidactylus brookii Gray 4.25 mm (4.1 mm);
Emys orbicularis (L.) (*Emys orbicularis* (*europaea*)) small specimen 4.3 mm;
Lygosoma 5 mm;
Lacerta viridis (Laur.) 5.8 mm;
Naja melanoleuca Hallow 7.0 mm;
Varanus niloticus (L.) 12.5 mm (Dubois, 1919 *b*, p. 713 gives 5.8 mm);
Uromastix 12.7 mm;
Tupinambis 15.5 mm;
Iguana 16.6 mm;
Alligator mississipiensis Daud. (*Alligator lucius* (*mississipiensis*)) 20 mm.

With regards to Aves we find in Franz (1934, pp. 1127-1128, 1198) the following values about the eye size:

Passer domesticus L. 7.4 mm;
Apteryx 8 mm;
Motacilla alba L. 8.1 mm;
Delichon urbica (L.) (*Hirundo urbica*) 9.5 mm;
Turdus pilaris L. 13.0 mm;
Corvus corone L. 20 mm;
Eudyptes crestatus (J. F. Miller) (*Eudyptes chrysocome*) 25 mm;
Struthio according to diverging statements 44, 45 and 52 mm.

For the absolute measurement of the eye size in Mammalia Franz (1934, pp. 1200-1202, 1209, 1257, 1258, 1260-1262) gives the following figures 1):

Notoryctes typhlops Stirling less than 1 mm;
Talpa europaea L. ca 1 mm;
Rhinolophus hipposideros (Bechst.) ca ("rund") 1 mm;
Plecotus auritus (L.) ("Ohrenfledermaus") 2.3 mm;
Myotis myotis (Borkh.) 2.8 mm;
Mus musculus L. ("Hausmaus") 3 mm;
Ornithorhynchus 6 mm;
Erinaceus europaeus L. 6.5 mm;
Rattus rattus (L.) ("Ratte") 6.75 mm;
Cynopterus 7.5 mm;
Tachyglossus (*Echidna*) 8.5 mm;
Pterocyon 11 mm;
Hypsignathus 13 mm;
Tarsius 13 mm;
Vulpes vulpes (L.) (*Canis vulpes*) 16 mm;
Oryctolagus cuniculus (L.) according to different statements 16.1 and 16.5 and 17.9 mm;
Gorilla 20 mm;
Thalarctos maritimus (Phipps) (*Ursus maritimus*) 21.5 mm;
Orycteropus 22 mm;
Dicotyles tajacu L. (*Pecari tabaju*) (*Dicotyles torquatus*) 22.4 mm;
Homo sapiens L. 24.2 mm;
Acinonyx jubatus (Erxl.) (*Cynailurus jubatus*) 32 mm;
Panthera leo (L.) (*Felis leo*) 35 mm;
Zalophus californianus (Less.) (*Eumetopias*, *Otaria californianus*) 39 mm;
Elephas indicus L. 41 mm;
Giraffa camelopardalis (L.) 47.5 mm;
Equus caballus L. 48.7–51.0 mm;
Equus (*Hippotigris*) *zebra* L. 49.5 mm;
Mirounga leonina (L.) (*Macrorhinus leoninus*) 63.3 mm;
Balaena mysticetus L. 70.5 mm;
Megaptera novae angliae (Botowski) (*Megaptera boops*) 92 mm;
Balaenoptera physalus (L.) 120 mm;
Balaenoptera musculus (L.) 145 mm.

As Franz (1934, p. 1200) observes, the absolute size of the eye both of the Mammalia and the Pisces is extremely varying.

As can be deduced from the above figures, there is a connection between the absolute sizes of the eye and the body, in this sense that the largest eyes (in absolute sense) occur in the largest animals (in absolute sense), as in the Cetacea among the Mam-

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1) For the absolute size of the eye ball in Primates see: A. H. Schultz (1940), Amer. J. phys. Anthrop. **26**, pp. 389-408. (Postwar addition in the manuscript)

malia, in *Struthio* among the Aves and in the large Euselachii among the Pisces. FRANZ (1934, p. 1128) mentions this reciprocity between absolute size of the eye ball and absolute size of the body, in Aves, as has been more closely investigated for some species of Ducks.

The relative size of the eye ball

The data most valuable for our purpose are lacking, namely the data concerning the relation between the size of the eye ball and the skull or the head. The data of GREGORY (1933) may refer to this relation, but this is nowhere expressly mentioned in this publication. We shall therefore deal with these data in the discussion about the relation between the size of the eye ball and the size of the body.

The relative size of the eye ball has been determined in several ways. A relation has been ascertained between the weight of the eyes and the weight of the brain, between the size of the eyes and the size of the brain, between the size of the eye and the size of the masticatory muscles, between the size of the eye and the length of the body, between the size of the eye and the surface of the body and between the size of the eye and the weight of the body.

The relation between the weight of the pair of eyes and the weight of the brain is in *Passer domesticus* L. ca 1 : 2.5, in the juvenile *Hirundo rustica erythrogaster* Bodd. (*Chelidon erythrogaster*) ca 6 : 5 and in *Aphelocoma californica* (Tigors) ca 6.6 : 5.2 (FRANZ, 1934, p. 1128).

The relation between the size of the eyes and the size of the brain is also stated. For instance, the eyes in Elasmobranchii ("Knorpelfische") are rather large, often larger than the brain (FRANZ, 1934, p. 1009). OWEN (1866 II, pp. 135/136) already mentioned, that in Aves the eyes are large, both compared to the brain, and compared to the whole head.

Sometimes there is also a relation between the development of the eyes and also of the orbita, and the development of the masticatory muscles. The great development of the musculus masseter and of the musculus temporalis in some subterraneously living Rodentia is attended by a reduction of the eye and a small orbita; these are the result of a lack of space ("Raumknappheit") (WEBER, 1927 I, p. 183; FRANZ, 1934, p. 1262). We may add to this that among the Rodentia there are also genera, as *Jaculus* (*Dipus*), *Alactaga* (*Scirtetes*) (see my fig. 26) and *Pedetes*, where the influence of the large eyes, besides the influence of the brain on the build of the skull, is conspicuous (STADTMÜLLER, 1936, p. 972).

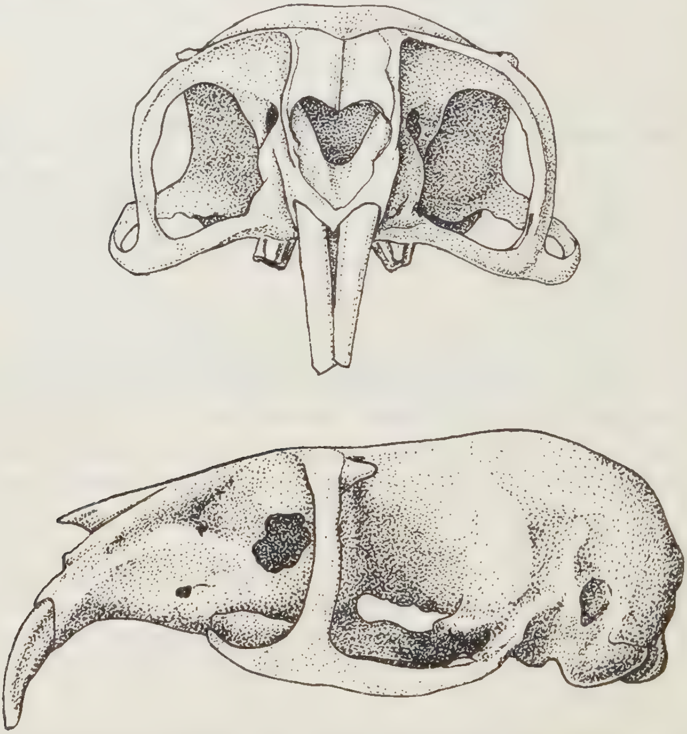

Fig. 26. *a. Alactaga saliens* (Gmel.). Skull seen in front view. R.M.N.H. Leiden, 1869. 2.0×. Original drawing by C. F. A. BRUIJNING. *b. Alactaga saliens* (Gmel.). Skull seen from the left side. R.M.N.H. Leiden, 1869. 2.0×. Original drawing by G. VAN GELDEREN.

The relative size of the eye ball as related to the length of the body, surface of the body, size of the body and weight of the body

Figures and observations about the relation between the size of the eye ball and the length of the body, the surface of the body and the rather vague conception of the size of the body and the weight of the body are rather numerous. For various reasons it does not seem advisable to try and bring these data concerning the whole body under separate headings.

In stages of development

In young stages of Vertebrata the relations between the size of the eye ball and the size of the body are different from the adult stages, because in Vertebrata generally, during development, the growth of the eye does not keep pace with the growth of the whole body in general, so that the relative size of the eye ball varies with the stage of development and the stage of growth (Franz, 1934, pp. 1006, 1020).

E.g., the length of the eye in an *Ammocoetes* of a body length of 6 cm is hardly ("knapp") 0.4 mm (that is about 0.66 % of the length of the body); with a body length of 18 cm, the length of the eye is 0.8 mm (0.44 %); during the quick metamorphosis a body length of 16 cm and an eye length of 2 mm is found (1.25 %). This phenomenon is found in all Petromyzonidae. During the larval life of *Lampetra* (*Petromyzon*) the development of the eye is therefore checked or slowed down (Franz, 1934, p. 1006). In the ontogeny of the related *Geotria*, the eyes have increased in each following stage and finally the eyes are even very large; this last stage has nocturnal habits or dwells in deep regions (Franz, 1934, p. 1007). In the cave dwelling Pisces of the genera *Lucifuga* and *Stygicola* the size of the eye decreases continually ("ständig") after birth (Franz, 1934, p. 1056). According to Gregory (1933, pp. 327, 422/423, 428, 445, 450) it is usual among Teleostei that the eyes are very large in the late embryos, larvae and fry; as the fry becomes larger, the eye becomes relatively smaller; thus in the embryonic stages of most Teleostei the accelerated eye dominates the head; but as growth proceeds the eyes are retarded and decrease in relative size.

In the development of *Typhlomolge* we find an eye length of 0.3 mm in a body length of 30 mm (so here the eye length is 1 % of the body length) and an eye length of 0.5 mm in a body length of 90 mm (0.55 %), so a decrease in relative size (Franz, 1934, p. 1083).

In a specimen of *Typhlops* with a body length of 10 cm the eye has 3/4 of the size of the eye ("erst 3/4 so gross") in a specimen with a body length of 21 cm (Franz, 1934, p. 1116).

Franz (1934, p. 1128) says that in Aves as in many other animals, the eye of younger, not yet full-grown specimens is relatively larger than the eye of adult specimens of the same species. Franz gives as examples that in a *Struthio* with the size of a *Corvus*, the eye is 28.5 mm large, which is relatively larger than in an adult specimen and at the same time also larger than in any *Corvus*. In an *Apteryx* with the size of a *Gallus* the eye is already 8 mm large, that is as large as in an adult *Apteryx*.

The fact that the size of the eye also depends on the age occurs in other groups as well and makes the relation between the eye size and the body size, *etc*., yet more intricate than it is already owing to all sorts of circumstances still to be discussed below (Franz, 1934, p. 1020).

In adult animals

For adult specimens a number of data are available concerning the relation between the rostro-caudal (horizontal) diameter of the eye ball and the length of the body, and one or two exact data about the relation between the weight of the eyes and the weight of the body.

Concerning Pisces Franz (1934, pp. 998, 1007-1009, 1019, 1054/1055, 1059, 1063, 1064) gives the following ratios for the rostro-caudal (horizontal) diameter of the eye ball and the body length; I give the figures in percents and have arranged them in order of increasing value:

Bdellostoma polytrema Girard (*Bdellostoma dombey*) 0.2 % (1 in 500 mm);
Protopterus 0.67 % (2 in 300 mm);
Cetorhinus maximus (Gunner) (*Selache maxima*) 0.75 % (63 in 8420 mm);
Lepidosiren 0.8 % (10 in 1240 mm);
Muraena anguilla L. (*Anguilla vulgaris*) 0.96 % (5 in 520 mm);
Geotria ca 1 %;
Somniosus microcephalus (Bl. Schn.) (*Laemargus borealis*) 1.7 % (ca 33 probably in 2000 mm);
Lampetra fluviatilis (L.) (*Petromyzon fluviatilis*) 1.7 % (4.9 in 290 mm);
Mordacia lapicida (Rich.) 1.8 % (3 in 170 mm);
Hypotremata (Batoidei, Rajidae) and *Squatina* 2–2.6 %;
Eulamia (*Carcharias*) 2.5 % (35 in 1400 mm);
Isurus nasus (Bonnaterre) (*Lamna cornubica*) 3 % (45 in 1500 mm);
Scyliorhinus (*Scyllium*) 3.6 % (16 in 450 mm);
Squalus (*Acanthias*), *Mustelus* and *Galeorhinus* (*Galeus*) 4–4.3 % and 6.6–7.1 % (15–25 in 350–380 mm; but according to Franz, p. 1019: 1/20–1/35);
Etmopterus (*Spinax*) 4.5 % (17.5 in 390 mm);
Chimaera 5 % (35 in 700 mm);
Ostracion 8 % (8 in 100 mm).

For Amphibia Franz does not give a single exact ratio for the rostro-caudal (horizontal) eye length and the body length in adult animals. Franz (1934, p. 1083) only states a ratio of 1.4 % (1.3 in 90 mm) for a larva of *Typhlotriton*.

Concerning Mammalia[1]) Franz (1934, p. 1201) gives the following ratios about the rostro-caudal (horizontal) length of the eye and the length of the body, expressed by me in percents:

Balaena mysticetus L. 0.35 % (70.5 in 20000 mm);
Balaenoptera musculus (L.) 0.47 % (145 in 31000 mm);
Balaenoptera physalus (L.) 0.55 % (120 in 22000 mm);
Megaptera novae angliae (Botowski) (*Megaptera boops*) 0.61 % (92 in 15000 mm);
Phocaena ca 2 %;
Mirounga leonina (L.) (*Macrorhinus leoninus*) 2.1 % (63.3 in 3000 mm);
Pippestrellus (*Vesperugo*) 2.3 %;
Pteropus 5.5 %.

Less exact are these ratios, where Franz (1934, pp. 1262, 1263) states that the eye of *Manis javanica* Desm. has but the size of a pea ("nur erbsengross") to a body length of more than 800 mm, and in *Platanista gangetica* (Lebeck) the eye reaches hardly the size of a pea ("nur knapp Erbsengrösse") with a body length of 1800 mm.

In order not to interrupt the discussion of the factors that influence the ratios between the size of the eye and the length of the body, the surface of the body, the size of the body and the weight of the body, we shall first mention some figures concerning the weight of the eyes in relation to the weight of the body.

The weight of the eyes of *Strix aluco* L. (*Syrnium aluco*) is 1/32 of the body weight, whereas in other equally large Birds it is 1/90 (Franz, 1934, p. 1128).

Reckoning by the body weight it is *Felis catus* L., that has relatively the largest eyes, then follow: *Canis familiaris* L., *Ovis aries* L., *Bos taurus* L. dom. juv., *Equus caballus* L., *Homo sapiens* L., *Bos taurus* L. dom. ♀, *Sus scrofa* L. and *Bos taurus* L. dom. ♂ castr. (Franz, 1934, p. 1201).

An examination of the relation between the size of the eye and the size of the body has resulted in the conception of the so-called ratio inversa of Haller, *viz.*, that with increasing absolute body size, the relative eye size decreases (Franz, 1934, pp. 1020, 1201). So there is no proportional relation between the receptive surface of the eye and the general body surface (Dubois, 1897 *a*, p. 21; 1897 *b*, p. 355; 1897 *c*, p. 14). Many examples can be found in the above list of ratios. So the effect of this ratio is, as Dubois (1897 *a*, pp. 21, 22; 1897 *b*, pp. 355, 356; 1897 *c*, p. 14; 1913, p. 607; 1914 *a*, pp. 661/662; 1914 *b*, p. 342; 1917, p. 290; 1918 *a*, p. 1424; 1918 *b*, p. 1336) formulated, that small animals have relatively large eyes and that large animals have relatively small eyes in comparison to their body weight; here exists a relation of a similar nature as with regard to the quantity of the brain, which is likewise relatively small for animals of high body weight. According to Dubois (1897 *a*, pp. 21/22; 1897 *b*, pp. 355/356; 1897 *c*, p. 14) this phenomenon is most striking when comparing closely related animals. He gives the following four examples. In *Panthera leo* (L.) the linear size of the images on the retina is only 1.67 times as large, the surface of these images 2.8 times as large as in *Felis catus* L., whereas the body weight of *Panthera leo* (L.) is about 36 times the body weight of *Felis catus* L. and the body surface of *Panthera leo* (L.) about 11 times the body surface of *Felis catus* L. (the retina in *Felis catus* L. is relatively about four times larger than in *Panthera leo* (L.)). The linear size of the images on the retina of *Sibbaldus musculus* (L.) (*Balaenoptera Sibbaldi*) is only 2½ times that of the images on the retina of *Phocaena phocoena* (L.) (*Phocaena communis*), whereas the linear dimensions of their bodies are in proportion about 10 – 20 to 1. The images on the retina of *Pandion haliaetus* L. are only $1^2/_3$ times as long and broad as those of *Falco tinnunculus* L., although the linear dimensions of the body of *Pandion haliaetus* L. are 3 or 4 times larger than those of *Falco tinnunculus* L. Without exception the smallest individuals of the various specimens of *Equus caballus* L., *Bos*, *Ovis aries* L., *Sus*, *Canis familiaris* L., *Felis catus* L. and *Oryctolagus cuniculus* L. have relatively the largest eyes.

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[1]) For the relative size of the eye ball in Primates see: A. H. Schultz (1940), Amer. J. phys. Anthrop. **26**, pp. 389-408. (Postwar addition in the manuscript)

As examples of the ratio inversa of Haller Franz (1934, pp. 1019, 1020) mentions emphatically that in *Somniosus microcephalus* (Bl. Schn.) (*Laemargus borealis*) and in *Cetorhinus* (*Selache*) the eye is large in the absolute sense, but in relative sense the eye is small in these large animals. Thus *Felis silvestris* Schreb. ("Wildkatze") has relatively larger eyes than *Lynx lynx* (L.) ("Luchs") and the latter again relatively larger eyes than *Panthera leo* (L.). Again, the relative eye size among the marine Mammalia drops from about 1/50 in *Phocaena* to 1/200 in *Balaenoptera physalus* (L.) (Franz, 1934, p. 1201). And again the eye of *Sus scrofa* L. is also relatively small and the eye of *Homo sapiens* L. relatively large (Franz, 1934, p. 1201).

This ratio inversa of HALLER is often reversed. FRANZ (1934, p. 1201, see also pp. 1259, 1261) mentions as an example of such reverse the Chiroptera: the relation between the eye size and the body size is 1/44 in *Pippestrellus* (*Vesperugo*), and in the larger *Pteropus* 1/18; the eye of the Microchiroptera is generally very small (*vide* the figures mentioned above); even the largest eye, *viz.*, of *Desmodus*, is far behind in size, compared with that of the Megachiroptera (Macrochiroptera), where the eye of *Cynopterus* (7.5 mm) is called small and that of *Pterocyon* (11 mm) of medium size ("mittelgross"). In this way the passages in WEBER (1927 I, pp. 183/184) can be understood, that the eye of the Mammalia is sometimes proportional in its size to the body size, as in Ungulata and Cetacea, but that on the other hand we find small eyes in large animals, as in *Elephas* and *Odobenus*.

An explanation of this reversion of the ratio inversa of HALLER may be found in the fact that the size of the eye ball, apart from the relation to the body size is also connected with the speed of locomotion, the way of finding food and the intensity of light of the milieu and with the milieu in general. We will insert these ways of explanation in the now following attempts to arrive at a formula, in which the regular relation of eye size and body length, body size and body weight is expressed.

DUBOIS who has taught us so much about a clear understanding of the connection between body weight and brain weight and has laid down this connection in a formula, also gives a number of directions about and a formula for such a regular connection between eye size and body size and body weight. These last points we will discuss in the same order as we did for the brain, *viz.*, for the two sexes, for various individuals of the same species, for different races, for homoneuric animal species and for heteroneuric animal species, and finally we will wind up with a survey of the relation between eye size and body size in the different classes of the Vertebrata and in the main groups within these classes.

In both sexes

No data are found in literature.

In various individuals of the same species

About the relations of the size of the eye to the body size for individuals within a species hardly any direct data are available according to DUBOIS (1919 *a*, p. 506; 1919 *b*, p. 714). He adds that in *Canis familiaris* L. the diameter of the eye only varies from 20 to 23 mm, whereas the body weight varies from 5 to 40 kilograms, *i.e.*, about as the fifteenth power root of this weight. For the exponent of relation r_0 we find here 0.1344, which means the individual ocular exponent of relation has decreased in the same ratio, with respect to what is observed between different species, as the encephalic exponent of relation. DUBOIS remarks in passing that the found value lies nearer half 0.28 than half 0.22. According to DUBOIS (1930, p. 279) this ocular exponent of relation is of about half the value of the exponent valid between different species, consequently also of half the value of the encephalic exponent of relation, valid for individuals within a species.

In different races

It does not appear from the data in literature, in how far in the wording of the relation between the size of the eye to the body size in various individuals of the same species, as discussed above, also individuals of different races are included.

It is a well-known phenomenon, that the eye size of domestic animals is less than that of their related wild forms. When tame and wild forms are races of one and the same species, they come under this head. The phenomenon is well-known for the domesticated *Oryctolagus cuniculus* (L.) compared with the wild related form, for *Anas platyrhyncha* L. dom. compared with the wild Duck and also for *Putorius furo* (L.), the Ferret compared with *Putorius putorius* (L.) (FRANZ, 1934, pp. 1128, 1201; BÖKER, 1937, p. 193).

In homoneuric species of animals

In his older publications, in which DUBOIS (1913, pp. 607-609; 1914 *a*, pp. 662-664; 1914 *b*, pp. 342-345) tries to fix the relation between the size of the eye to that of the body by calculating an exponent of correlation, DUBOIS states that instead of comparing the simple diameter of the eye ball (which in its shape and in the thickness of the sclerotica is variable) it is preferable to compare the linear sizes of the images on the retina. Comparing linear sizes of the images on the retina of *Sibbaldus musculus* (L.) (*Balaenoptera Sibbaldi*) and *Megaptera novae angliae* (Botowski)

(*Megaptera boops*), the lengths of the images are proportional to $\sqrt[7.6]{S}$; for *Hyperoodon ampullatus* (Forst.) (*Hyperoodon rostratus*) and *Phocaena phocoena* (L.) these diameters increase as $\sqrt[7.5]{\frac{S}{s}}$; for *Panthera leo* (L.) and *Felis catus* L. the proportion of lengths of the images in the eyes is exactly equal to $\sqrt[7.5]{\frac{S}{s}}$ also; an equal relation is found between *Pandion haliaetus* L. (Sea-eagle) and *Accipiter gentilis* (L.) (Hawk). This is the reason why Dubois concludes that linear dimensions of the images vary as $\sqrt[7.5]{S}$ or $S^{0.133\cdots}$.

If the coefficient of cephalisation is the same or if only there is no great deviation in the coefficient of cephalisation, the general validity of this relation is obvious. The shapes of the bodies can then even be greatly different.

In his publication of 1917 Dubois (1917, p. 290) says that the relation between the size of the eye to the body size is $l^{1/3}$ or $S^{1/9} = S^{0.11}$.

In his later publications Dubois (1918 *a*, pp. 1424/1425; 1918 *b*, p. 1337; 1919 *a*, p. 506; 1919 *b*, p. 714; 1920 *a*, p. 87; 1920 *b*, p. 628; 1920 *c*, p. 670; 1930, p. 278) says that it can be derived from numerous determinations of the size of the eye of higher and lower Vertebrata that in animal species of the same form but of different sizes, thus in large and small homoneuric species, the area of the retina and also the diagonal area measure of the eye ball, varies on an average in proportion to $\left(\frac{P}{P_1}\right)^{5/18}$. The exponent of relation thus is 5/18 or 0.28 or 0.277 or 0.27, that is half the exponent of relation for the brain weight. The area of the retina in general does not vary in proportion to the area measure of the whole animal, *viz.* much less strong than this area measure (Dubois, 1920 *a*, p. 87; 1930, p. 278).

This conclusion about the exponent of relation for the area of the retina is based in the paper of 1919 (1919 *a*, pp. 504-506; 1919 *b*, pp. 712-714) on a number of considerations. Dubois fixed in this paper the value of the exponent of relation at 0.277 and attributed the deviations of the found exponents (varying from 0.2390 till 0.3290) to the facts that the compared species are not all perfectly homoneuric, that also the specimens are not always typical for their species, that the body weight was not always directly determined and that the retinal area can only be calculated from the diameter of the eye (in one case the weight of the eye) in approximation. The exponent of relation r_o is calculated from $\left(\frac{P}{p}\right)^{r_0} = \frac{O}{o}$, where P and p denote the body weights, and O and o the retinal areas, more accurately the areas of section of the eye ball proportional to these in approximation.

In heteroneuric species of animals

In Dubois we do not find any attempt to arrive at an exact formulation about the relation between the size of the eyes and the body size or the body weight in heteroneuric animal species. However, we are able to deduce one thing and another about the size of the eye from the factors which, according to him, influence the value of the coefficient of cephalisation. For we have seen, that in his older publications Dubois connects the value of the coefficient of cephalisation and the development of the organs of sense (the organs of sight, hearing, touch, smell), the development of the muscles, the activity, the body length, *etc.* We also saw in these publications that the influence of the eye in itself remains restricted.

Consequently, if a relation (albeit a restricted relation) exists between eye size and brain size, the development of factors such as the muscular system, the activity, *etc.* will play a part in the expression of the nature of the relation between eye size and body size and in its exact formulation, because these factors influence the brain size and this is connected with the body size.

So we have seen that there is a connection between brain size and body length. We have already discussed that there is also a relation between eye size and body length (the ratio inversa of Haller). We have seen that there is a connection between brain size and the development of the muscular system. We shall see that there is a connection between eye size and speed of locomotion ("Lokomotionsmass") (the ratio of Leuckart). We have seen, that there is a connection between brain size and the development of the organs of hearing, touch and smell. We shall discuss that there is a connection between eye size and the way of seeking food. Moreover we shall amply discuss the relation between the eye size and the intensity of light of the milieu and the milieu in general.

The relation between the eye size and the speed of locomotion ("Lokomotionsmass") is known as the so-called ratio of LEUCKART (FRANZ, 1934, pp. 1127, 1201).

Among the littoral Elasmobranchii (Plagiostomi), the forms living on the bottom of the sea (Hypotremata, *Squatina*) have smaller eyes than the more pelagically living predatory Pisces (FRANZ, 1934, p. 1020; HALLER VON HALLERSTEIN, 1934, p. 16). The relation inferred here with the way of seeking food will boil down to a relation with the speed of locomotion. The fact that *Etmopterus* (*Spinax*) and *Chimaera* have very large eyes (GREGORY, 1933, p. 103; FRANZ, 1934, pp. 1017, 1018; HALLER VON HALLERSTEIN, 1934, p. 150) may also come under this aspect and maybe *Callorhynchus* as well (HOLMGREN & STENSIÖ, 1936, p. 335; *vide*, however, FRANZ, 1934, p. 1019). It is undoubtedly a question of the speed of locomotion that the eyes of the generally sluggish Marsipobranchii (Cyclostomata) as *Lampetra* (*Petromyzon*) may be called normally large and those of *Geotria* of a rather small relative size ("wohl etwas geringe relative Grösse") (FRANZ, 1934, pp. 1002, 1007).

Struthio, a quick courser, even if no flyer, has the largest eyes among the Aves, larger than in any other terrestrial Mammal and surpassed in size only by some large Pisces and aquatic Mammalia (FRANZ, 1934, pp. 1127/1128). Thus *Delichon urbica* (L.) (*Hirundo urbica*) with its great flying-speed has relatively very large eyes (FRANZ, 1934, p. 1128).

Among the Mammalia the ratio of LEUCKART is not so clearly expressed, because there are too many other factors joining in (FRANZ, 1934, p. 1201). The relation to be discussed below, between the speed of locomotion of the various groups of the Carnivora, and the size of the orbita will be expressive of the relation between the speed of locomotion and the eye size.

The smaller size of the eyes in domesticated Aves and Mammalia compared with their related wild forms, discussed above, will undoubtedly be due to a decreased speed of locomotion.

In literature eye size and the way of seeking food are also associated. We have seen above, that this relation is used to explain the difference in size of the eyes in littoral Elasmobranchii (Plagiostomi). In the example given, a difference in the speed of locomotion was connected with it.

Whether this is also the case in *Apteryx* and in the ant-eating

Mammalia is not clear to me. The eyes of *Apteryx* and of the Dinornithidae (Moas) may be called relatively small or very small, while the eye of the Aves can generally be called large, sometimes even colossal (STRESEMANN, 1933, pp. 748, 751; HALLER VON HALLERSTEIN, 1934, pp. 16, 155, 167, 168, 192; FRANZ, 1934, pp. 1095, 1127, 1128). *Apteryx*, in finding its food, is guided by the tactile sense of its bill and not by its sight; consequently the eye is rudimentary (FRANZ, 1934, p. 1128) (see my fig. 57). In Caprimulgidae with their wide mouth fissure the enlarged eye is also undoubtedly connected with the way of seeking food (BÖKER, 1937, p. 97) (see my fig. 33).

A connection with the way of seeking food is also probably present in Monotremata, Xenarthra, Pholidota and in *Orycteropus* with their small eyes (FRANZ, 1934, pp. 1257, 1262). According to FRANZ (1934, p. 1262) the eye of *Orycteropus* is noticeably ("erheblich") large for an Edentate, and especially for an "Ameisenzüngler" as well, both among the Edentata and among other groups, as for instance *Tachyglossus* (*Echidna*).

The eye size bears an intricate relation to the intensity of light of the milieu in which the animal lives. In a dim milieu the eyes are sometimes very large, but they can be also small and rudimentary. Even within small systematic groups both possibilities are sometimes realised.

Thus FRANZ (1934, p. 1052) states for the Amblyopsidae that the phyletically increasing life in darkness ("Dunkelleben") – in so far as no enlargement of the eyes occurs – has first of all caused a decrease in the size of the eyes ("zunächst nur kleiner") before other internal changes occur. Also the Stomiatidae, deepsea forms with telescope-eyes, have sometimes small, sometimes large eyes (FRANZ, 1934, p. 1050). GREGORY (1933, pp. 157, 439, fig. 54) states, that among the Stomiatoidea, the eyes in *Sternoptix* are huge and in *Cyclothone* very small. Also among the Muraenidae (Anguillidae) we find several deepsea forms, partly with large eyes (*Coloconger*, *Synaphobranchus*), partly with small eyes (*Avocettina*) (FRANZ, 1934, p. 1055).

Also among the Mammalia that live in darkness we find either small eyes (Insectivora, Chiroptera), or large eyes, which is the case in Lemuroidea (Prosimiae), as *Daubentonia* (*Chiromys*) and *Tarsius* (not however in *Lemur*, which are diurnal animals) (WEBER, 1937 I, pp. 183/194; FRANZ, 1934, pp. 1263, 1264).

Of Vertebrata with large eyes, living in a dim milieu, there are many examples, some of which I will mention.

The deepsea forms among the Elasmobranchii (Plagiostomi) show a maximum eye size and among the littoral Elasmobranchii the eye size is dependent on the intensity of light ("Lichtfülle") of the milieu (Franz, 1934, pp. 1019/1020). Thus *Scyliorhinus* (*Scyllium*) a species, which prefers rather dim light for its activities ("eine wohl ziemlich im Dunkleren sich betätigende Art"), has larger eyes than *Mustelus* (Franz, 1934, p. 1020). Also among the Teleostei we find many deepsea forms with large or very large eyes (Gregory, 1933, p. 299; Franz, 1934, pp. 1037, 1048, 1049, 1056, 1057, 1058). The body length of the deepsea forms with telescope-eyes among the Teleostei being 12 cm at the utmost, the eye is consequently soon relatively large (Franz, 1934, p. 1029). Also among the freshwater forms among the Teleostei, which live in great depths, there are found forms with rather large, that is normally large eyes, as *Coregonus* and *Salmo salvelinus* L. (Franz, 1934, p. 1036).

Large eyes are also found once or twice among the Caudata (Urodela), which should be due to a way of living in semidarkness, as in some species of the genus *Hydromantes* (*Spelerpes*) (Franz, 1934, pp. 1082, 1083). In *Hyla maxima* (L.) the eyes are exceedingly large; this species is active at night (Böker, 1937, p. 19).

Also among the Aves large eyes are met with as an adaptation to dusk and darkness ("eine Anpassung an die Dämmerung bis Dunkelheit"), as in Striges and in *Podargus*. Besides, *Erithacus rubecula* (L.) and *Scolopax rusticola* L. have somewhat enlarged eyes; both are adapted to the shade of the wood (Franz, 1934, p. 1128).

We have seen already that several Lemuroidae (Prosimiae) (the species of the genus *Lemur* excepted) have large eyes, an adaptation to their living in darkness. The huge eyes of *Phoca vitulina* L. may also be due to this (Haller von Hallerstein, 1934, p. 192).

There are also many examples of small eyes in animals, living in a dim milieu.

The eyes of the deepsea ray *Benthobatis* are minute ("winzig") (Franz, 1934, p. 1019). Among the Teleostei there are fishes living in the dusk ("Dämmerungsfische") with relatively small eyes, such as *Cobitis*, *Misgurnus* and *Amiurus* (Franz, 1934, pp. 1036, 1037, 1062). The Gonostomidae is a family of deepsea fishes with increasingly reduced eyes (Franz, 1934, p. 1051).

Among the Sauria (Lacertilia) and Serpentes (Ophidia) there are some species with rudimentary eyes (Franz, 1934, p. 1095). Thus the eyes of burrowing Amphisbaenidae are rudimentary (Franz, 1934, p. 1106).

Also among the Mammalia the eyes of the blind subterraneously living species are minute ("winzig") and rudimentary; to a high degree this is the case in *Notoryctes typhlops* Stirling (Franz, 1934, pp. 1200, 1257). Odontoceti, as a rule living in greater depths, even in darkness, have smaller eyes than the Mystacoceti (Mysticetes) (Dubois, 1913, p. 613; 1914 *a*, p. 667; 1914 *b*, p. 349).

Finally, eye size and macromilieu in general have also been considered and connected, without mentioning a more immediate connection with the intensity of light of this macromilieu.

Thus Franz (1934, pp. 1079, 1082, 1083) assumes a connection between the aquatic living and the eye size in the Caudata (Urodela). According to him (Franz, 1934, p. 1079), the eye of the Salamandridae decreases in size in the order *Salamandra*, *Triturus* (*Triton*), *Ambystoma* (*Siredon*), in connection with the increasingly aquatic habits. Thus also, the eyes of *Megalobatrachus japonicus* (Temm.) (*Cryptobranchus japonicus*), Sirenidae and *Necturus* (*Menobranchus*) are small or very small (Franz, 1934, pp. 1083, 1084). We may possibly include the phenomenon that in Pisces, that leave water and move on land, the eyes are larger extremely so in *Periophthalmus* (Böker, 1937, p. 15). In this connection *Periophthalmus* with its greatly enlarged eyes is an exception among the Gobioidei, which generally have small eyes (Gregory, 1933, pp. 346, 439).

There are in literature very many data about the relative size of the eye ball and about the differences in size of the eye within smaller and larger systematic groups and between related groups mutually, without any explanation being given, as far as I know, based on one of the factors discussed above (body length, speed of locomotion, intensity of light of the milieu, *etc.*). Nevertheless, we shall give such data here.

The eyes of the Teleostei are in general relatively very large, sometimes huge (Haller von Hallerstein, 1934, pp. 16, 155, 192).

Gregory's comprehensive study about the skull of Pisces

(1933) gives a large number of stray remarks about the size of the eye. These remarks do not give many details and are not at all or only little suited for an exact determination of the size of the eye ball. It is not even stated if the absolute or relative size is meant and in the latter case with regard to what part of the body (head, skull or the whole body). Moreover, I am not always certain that the data about the eye size do not refer to the orbita now and then. For instance, in a number of cases the eye size in fossil Pisces is given (GREGORY, 1933, pp. 85, 112, 125, 131, 136, 137, 233/234), which cannot but refer to the orbita. In GREGORY's article then are found the following data about the size of the eye ball. The eyes of the Teleostei are large and dominant compared with those of the Euselachii (p. 131). Teleostei with large eyes retain this size in a later ontogenetic stage (p. 423). It is not always, however, that the Teleostei have large eyes, as we have seen above. Groups with small eyes are the Mormyroidea (at least *Gymnarchus*, *Mormyrops* and the Mormyridae) with their small and reduced eyes (pp. 173, 439), the Heterognathi (at least *Erythrinus*), with their eyes of moderate size (p. 183), the Opisthomi (at least *Rhynchobdella aculeata* (Bloch)) with their small eyes (p. 353) and the Lyomeri, where the eye is minute (pp. 439/440). Groups with large eyes among the Teleostei are the Percesoces (at least *Polynemus*) (p. 268) and the Trachinoidei (at least *Bathymaster signatus* Cope and *Astroscopus*) (pp. 358, 439). Then there are also systematic groups among the Teleostei, within which both large and small eyes occur. We have already come across some examples. Other groups are the following. Among the Chaetodontoidei, *Chaetodon* has large eyes, while *Angelichthys* and *Pomacanthus* have smaller eyes (pp. 278, 279). Among the Balistoidei, *Lactophrys* has enlarged eyes, while *Mola mola* (L.) has relatively small eyes, no doubt on account of the size of the body (pp. 286, 295). Among the Scombroidei the eye of *Luvarus* is large, the eye of the Carangidae is less well developed (pp. 304, 306). Among the Scorpaenoidei, the eye of *Sebastes*, *Sebastodes*, the Cottidae and the Triglidae, *etc.*, is big and dominates the head, while in *Synanceja* the eye is very small (pp. 322, 329, 332, 341). Among the Pediculati, the eye of *Aceratias macrorhynchus* Brauer and of *Haplophryne hudsonius* Beebe is large and bulging, while the eye of *Tetrabrachium ocellatum* Gthr, of the Ceratiidae and of *Oneirodes eschrichtii* Lütken is small (pp. 394, 401, 407, 410).

The average eye of the Caudata (Urodela) – we saw above that *Hydromantes genei* (Schl.) (*Spelerpes fuscus*) is an exception – is phyletically reduced, for the eyes of most of the Pisces are larger and also † *Branchiosaurus* has a larger eye (FRANZ, 1934, p. 1090). The eye of the Salamandridae is as a rule relatively smaller than in the Salientia (Anura), according to FRANZ (1934, pp. 1079, 1086); however, among the Salientia (Anura), the Aglossa have again very small eyes, particularly *Pipa pipa* (L.) (*Pipa americana*). According to BÖKER (1937, p. 19), the eyes of the Caudata (Urodela) are generally smaller than in the Salientia (Anura).

According to FRANZ (1934, p. 1090), the eyes of the Reptilia are, on an average, not larger than those of the Salamandrinae. According to HALLER VON HALLERSTEIN (1934, p. 162), however, the eye of the Reptilia is generally large. As an indication for this, we may also take the impressio bulbi oculi in the cerebral wall, discussed above, which is found in most Reptilia and furthermore also in the Aves.

As far as Aves are concerned, their eye ball is generally from large to very large (OWEN, 1866 II, pp. 135/136; BÖKER, 1937, p. 89). In the anatomic series † *Euparkeria capensis* Broom, one of the † Pseudosuchia, † *Archaeornis siemensii* (Dames), *Columba livia* (L.) dom. (*Columba domestica*) the eye increases in size (BÖKER, 1937, p. 89).

In the Mammalia the relative eye size undoubtedly lays behind that of the Aves, generally speaking (FRANZ, 1934, p. 1200).

d. The shape of the eye ball

We recall to mind the fact that in the above we only considered the horizontal rostro-caudal diameter of the eye ball, if indeed the different diameters were given. For a more exact consideration about the size of the eye ball we must also take into account the two other diameters of the eye ball, which need not be alike to the horizontal rostro-caudal diameter (*vide* above about the horizontal ellipticity ("Horizontalelliptizität")). It must be granted, however, that these two other diameters are not of the same importance as the horizontal rostro-caudal diameter, because the ventral wall of the orbita is sometimes absent and the eye is apt to bulge out of the orbita.

e. The size of the orbita

By the size of the orbita, when discussed in literature, is understood in my opinion, the surface of the lateral opening of the orbita, or where the ventral border is absent, the surface, when completed by the ventral border. The depth of the orbita, therefore, has nothing to do with it, in my opinion. Anyhow, we shall not include the depth of the orbita in the size of the orbita, in the following.

The absolute size of the orbita

I do not know any data, clearly referring to the absolute size of the orbita[1]).

The relative size of the orbita

Whereas the size of the eye ball with regard to a number of data about the body and parts of the body has been rather extensively examined, this is not the case with the orbita. In a great number of cases, however, we can arrive at a certain knowledge about the relative – and for that matter also about the absolute – size of the orbita, from the data concerning the size of the eye ball paying attention all the time to the relation between the size of the eye ball and the size of the orbita, as discussed above.

It is practically certain that all the data from literature, to be dealt with below, will refer to the size of the orbita in relation to the body length or to the vaguer notion of the body size.

In stages of development

In young stages of development of Teleostei the orbita is relatively very large, in still later ontogenetic stages the relative size of the orbitae decreases rapidly (GREGORY, 1933, p. 430).

In adult animals

It is impossible to illustrate with examples about the size of the orbita the distinctions given with the discussion of the relative size of the eye ball in specimens of the two sexes of one species, in several individuals of one species, in several races and in homoneuric animal species.

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[1]) For the absolute size of the orbita in adult Primates see: A. H. SCHULTZ (1940), Amer. J. phys. Anthrop. **26**, pp. 389–408; and in adult and young Gibbons and a few other Anthropoid Apes see: A. H. SCHULTZ (1944), Amer. J. phys. Anthrop. **2**, pp. 1–129. (Postwar addition in the manuscript)

We can only give a number of data about the size of the orbita in heteroneuric animal species, and even here, hardly illustrate the various factors which could be held responsible for the differences in the size of the eye ball (body length, activity, way of seeking food, intensity of light of the milieu and the macromilieu in general) with examples, now that the relative size of the orbita is concerned. Indirectly, however, we can deduce something from the respective data about the eye ball. The direct data are but the following.

Difference in speed of locomotion results in difference in the size of the eye and is reflected in the size of the orbita. According to MURR (see FRANZ, 1934, pp. 1201, 1280), the orbitae of the inert Ursidae are relatively smaller than those of the other Carnivora; the orbitae of the Mustelidae and Procyonidae are almost equally small; then follow each in its place ("nach Abstand") the Viverridae, Canidae, Hyaenidae and finally the Felidae; *Lynx* foremost and then *Felis* show the largest measure of the orbita (see my figs 6, 7 and 8).

In the discussion of the relation between the size of the eye ball and the macromilieu we also pointed to the greatly enlarged eyes of *Periophthalmus* compared with the other Gobioidei with their small eyes. Also the orbitae of *Periophthalmus* (see my fig. 41) are very large, while those of the Gobioidei are small in general (GREGORY, 1933, pp. 346, 347).

From the above follows that we can but give the data in literature about the relative size of the orbita and the differences in this size within larger and smaller systematic groups and between related groups mutually, without being able to explain this size and these differences in size.

Concerning Pisces most data have been taken from GREGORY (1933). For these data the same reservation holds good as had to be made for the data about the relative size of the eye ball (it is uncertain whether these data refer to the relative size and if so, with relation to what property of the body or part of the body they apply, *etc.*). GREGORY's data concerning the eyes of fossils we give below as if they were meant for the orbitae of these fossil Pisces. – The orbita of *Chimaera* is, like the eye itself, very large (HOLMGREN & STENSIÖ, 1936, p. 337). Among the † Palaeoniscoidei the orbitae of the Carboniferous forms are relatively enormous in relation to those of the Devonian † *Cheirolepis*, the "eyes" of which are not as large as those of typical Pisces and in relation to those of the Triassic † *Birgeria* (GREGORY, 1933, p. 112, fig. 13 B; HOLMGREN & STENSIÖ, 1936, pp. 399, 404). In the primitive fossil Chondrostei the orbita was small (GREGORY, 1933, p. 131). In the fossil Protospondyli or Holostei † *Acentrophorus* and the † Macrosemiidae the orbitae are large and dominant, as characteristic of Teleostei (GREGORY, 1933, pp. 85, 125, 131). – In the Teleostei in general a large eye is characteristic, as we have seen; thus also a large orbita is characteristic. In the primitive Teleostei of the group of the Isospondyli, as, *e.g.*, † *Pholidophorus* the orbita is much larger than in † *Macrosemius* (GREGORY, 1933, p. 136). As there are groups with large eyes as well as groups with small eyes and groups, in which large and small eyes occur side by side, among the Teleostei, the same groups occur among them with regard to the size of the orbita. To the groups with large eyes belong, as we have seen above, the Trachinoidei. Among the Trachinoidei, the orbita is large in *Pinguipes*, very large in *Dactylagnus* and huge in *Callionymus lyra* L.; on the other hand, the orbita is fairly large in *Trichodon*, but even small in *Astroscopus y-graecum* (C.V.) (see my figs 42 and 50) (GREGORY, 1933, pp. 356, 361, 364, 369, 371). But also in other groups of Teleostei the orbita is large. The orbita of the Microcyprini, at least of *Anableps tetrophthalmus* Bl. (see my fig. 40), and that of the Allotriognathi, at least of *Stylophorus chordatus* Shaw, is called enormous (GREGORY, 1933, pp. 220, 300). In the Salmonoidea, at least in *Galaxias*, the orbita is large (GREGORY, 1933, p. 156). In *Salmo* the eyes are relatively so large, that the orbito-temporal region of the skull occupies about a third of the length of the skull (HOLMGREN & STENSIÖ, 1936, pp. 486/487). In the Stomiatoidea, at least in † *Tomognathus mordax* Dixon, the orbita is very large (GREGORY, 1933, p. 157). In the Percoidei, at least in *Priacanthus*, the orbita has a huge size (GREGORY, 1933, p. 247). In the Salmopercae, at least in *Percopsis guttatus* Ag., and in the Blennioidei, at least in *Blennius* and in *Zoarces anguillaris* (Peck), the orbita is called large (GREGORY, 1933, pp. 232, 374, 375). In the Berycoidei, at least in † *Hoplopteryx lewesiensis* (Mantell), the orbita is relatively large (GREGORY, 1933, p. 233). In the Gymnotidae, at least in *Eigenmannia macrops* (Blgr), further in the Cyprinodontes, at least in *Fundulus* and finally in the Synentognathi, as

Tylosurus, *Hemirhamphus* and *Halocypselus* (see my fig. 27) the orbita is called fairly large (GREGORY, 1933, pp. 186, 221, 223). We saw before, that the groups of Teleostei with a small eye ball include among others the Heterognathi, at least *Erythrinus* (see my fig. 28), but in *Gasteropelecus* the orbita is large (GREGORY, 1933, p. 185). The third group is formed by small groups of Teleostei within which both large and small orbitae occur. Above we came to know the Scorpaenoidei as a group with representatives with large and with small eye balls. The Scorpaenoidei comprise as well representatives with large orbitae, as, *e.g.*, the Triglidae, in which the orbita is widely open and the eye dominates, beside the genus *Synanceja*, in which the orbita is very small (GREGORY, 1933, pp. 329, 341). But also the Clupeoidea and the Esocidae are groups, to which belong representatives with large orbitae and others with small orbitae. Among the Clupeoidea the orbita is very large (see my fig. 29) in *Dussumieria*, † *Ctenothrissa microcephala* (Ag.) and *Opisthoproctus*, large in † *Leptolepis* and *Tarpon atlanticus* (C. & V.), but small in *Coilia* (GREGORY, 1933, pp. 137, 139, 147, 151, 439). Among the Esocidae the orbita is fairly large in *Umbra krameri* Fitzinger, but small in *Esox masquinongy* Mitchill (GREGORY, 1933, p. 216) (see my fig. 30).

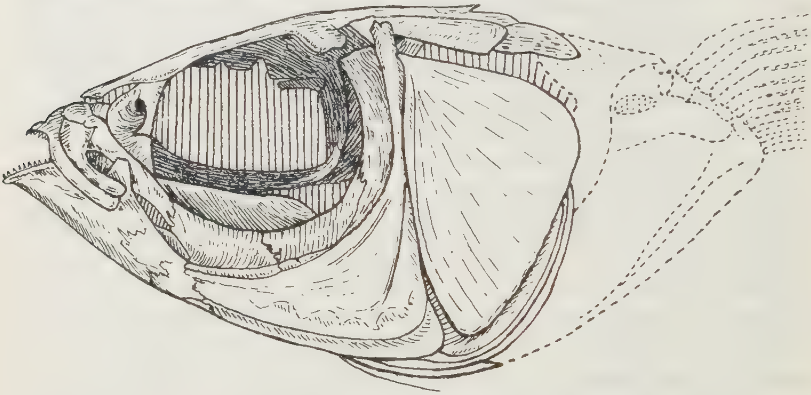

Fig. 27. *Exocoetus evolans* L. (*Halocypselus evolans*). Skull seen from the left side. After GREGORY (1933), fig. 101 on p. 222.

In the † Stegocephala the orbitae are generally rather large (see my figs 38 and 39); also in most of the Salientia (Anura) the orbitae are enlarged, whereas in Apoda (Gymnophiona) (see my fig. 31) they are very small (STADTMÜLLER, 1936, pp. 596, 601, 609).

In the † Pterosauria the orbita is large, relatively spoken (OWEN, 1866 I, p. 161). Also in the Chamaeleontidae (Chamaeleontia) the orbitae are very large (VERSLUYS, 1936, p. 779); according to FRANZ (1934, p. 1108), the eye of *Chamaeleo chamaeleon* (L.) (*Chamaeleon vulgaris*) is rather large (see my fig. 32).

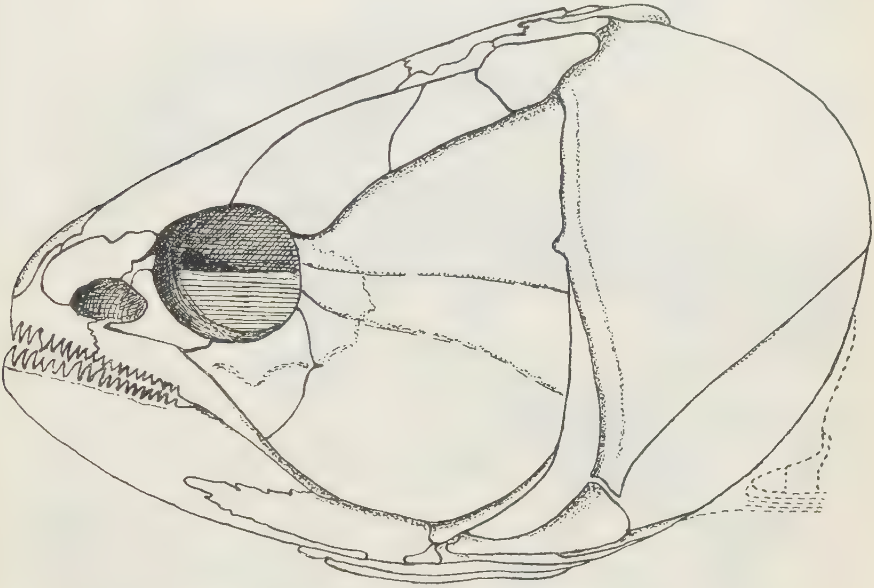

Fig. 28. *Erythrinus unitaeniatus* Spix. Skull seen from the left side. After GREGORY (1933), fig. 67 on p. 182.

In the Aves the orbitae are relatively large (OWEN, 1866 II, p. 62; ARIËNS KAPPERS, 1934, p. 463; MARINELLI, 1936, p. 819), which harmonizes with the size of the eyes (see my figs 33, 34, 36, 52 and also 13, 14 and 56).

Concerning the Mammalia[1]), DUBOIS (1930, pp. 287/288) points to the relatively much smaller orbitae in the slow † *Procamelus gracilis* Leidy in proportion to those of the fast *Lama guanicae* (Müller) (*Lama huanacus* Molina). Again the much less nimble ("körpergewandte") *Putorius putorius* (L.) (*Mustela putorius* L.) has relatively smaller orbitae than *Martes martes* L., which is an excellent climber ("Kletterer") and hunter of *Sciurus vulgaris* L. and than the equally nimble ("gewandte") *Martes foina* (Schreb.) and the excellently swimming *Lutra lutra* (L.) (Dubois, 1930, p. 288).

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[1]) For the relative size of the orbita in Primates see: A. H. SCHULTZ (1940), Amer. J. phys. Anthrop. **26**, pp. 389-408. (Postwar addition in the manuscript)

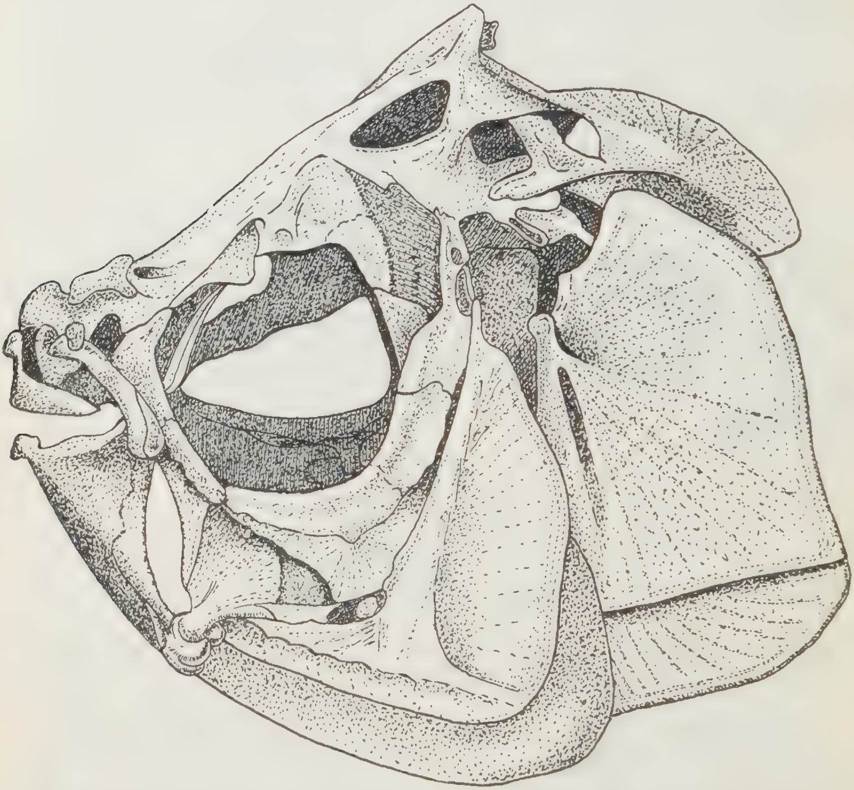

Fig. 29. *Dorosoma erebi* (Gthr). Skull seen from the left side. After Gregory (1933), fig. 39 on p. 147.

Furthermore we have seen above that in certain Rodentia the strongly developed masticatory muscles influence the size of the orbita.

f. The shape of the orbita

In the paragraph just concluded we discussed the size of the orbita. We saw in the introduction what should be understood by the size of the orbita. We saw too that in a great many cases we cannot speak of a vertical diameter of the orbita, because the orbita is not bordered ventrally by skeleton.

It remains therefore to discuss the depth of the orbita. The importance of the depth of the orbita with regard to the mutual position and the mutual distance of the orbita from left and right will come up for discussion in the next paragraph.

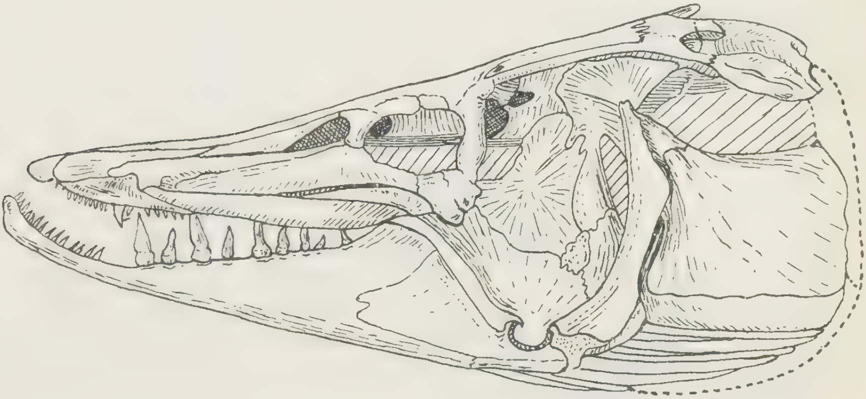

Fig. 30. *Esox masquinongy* Mitchill. Skull seen from the left side. After GREGORY (1933), fig. 95 on p. 215.

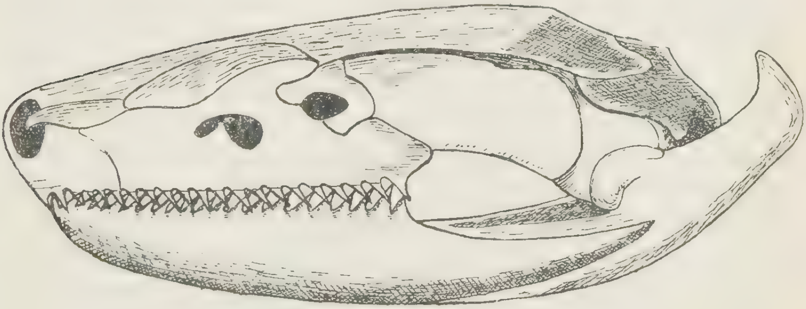

Fig. 31. *Ichthyophis glutinosus* (L.). Skull seen from the right side in mirror image. After VERSLUYS (1936) IV, fig. 468 on p. 624.

For the Elasmobranchii (Plagiostomi) FRANZ (1934, pp. 1018, 1019) states, that there are great differences in the depth of the orbita, connected with the size of the eye; but also with the form of the body.

I do not know in how far freely mobile, subcutaneous, rather small eyes with a primary cornea and a "primäre Brille", which are found in a number of Pisces and Amphibia, influence the depth of the orbita (FRANZ, 1934, pp. 993, 994).

g. The position

For our knowledge of the position of the orbita the position of the eye itself is not unimportant. We may even say, that the statement of a rostral position of the eye in the skull also means that the orbita is placed there. The same holds good for a caudal position, a position on the dorsal side of the skull, *etc.* It is different, however, with the statement, that the eye is directed forward or looks forward. This direction of the eye or rather of the axis of the eye can also occur in eyes placed far back in the skull. The same holds good for statements of other directions, to which the eye is directed or looks, as downward, upward, *etc.* Moreover, the direction of the eye ball or rather of the axis of the eye ball need not coincide with the direction of the axis of the orbita. Between

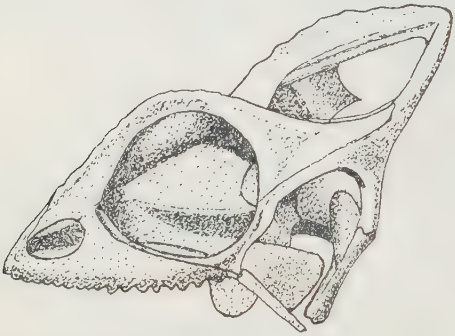

Fig. 32. *Chamaeleo.* Skull seen from the left side. After VERSLUYS (1936) IV, fig. 600 on p. 779.

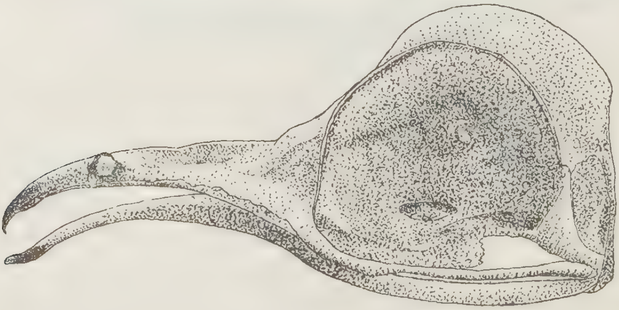

Fig. 33. *Caprimulgus europaeus* L. ♂. Skull seen from the left side. R.M.N.H. Leiden, Cat. ost. c. 2.0×. Original drawing by J. E. BEVELANDER.

these directions there may be small differences, but on the other hand not immaterial differences also occur (see my fig. 34). In this way apparently we should read Owen's statement (1866 II, pp. 62/63) about the Aves, that the orbitae are mainly directed laterally, while the eyes are directed a little forward and downward as well. In *Tarsius* the axes of the orbitae are at an angle

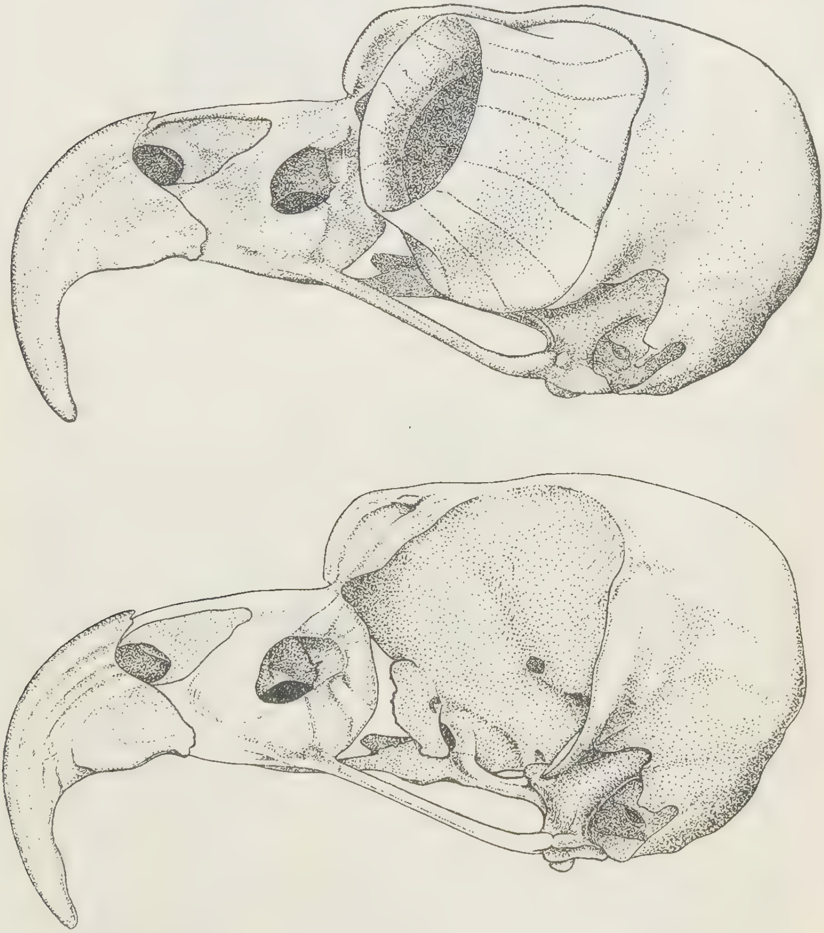

Fig. 34. *a. Bubo bubo* (L.). Skull seen from the left side with sclerotic ring. R.M.N.H. Leiden, 1866. 1.14×. Original drawing by G. van Gelderen. *b. Bubo bubo* (L.). Skull seen from the left side. R.M.N.H. Leiden, 1866. 1.14×. Original drawing by C. F. A. Bruijning.

of 19 degrees; and yet the eyes are almost completely directed forward (Franz, 1934, p. 1280) (see my fig. 35).

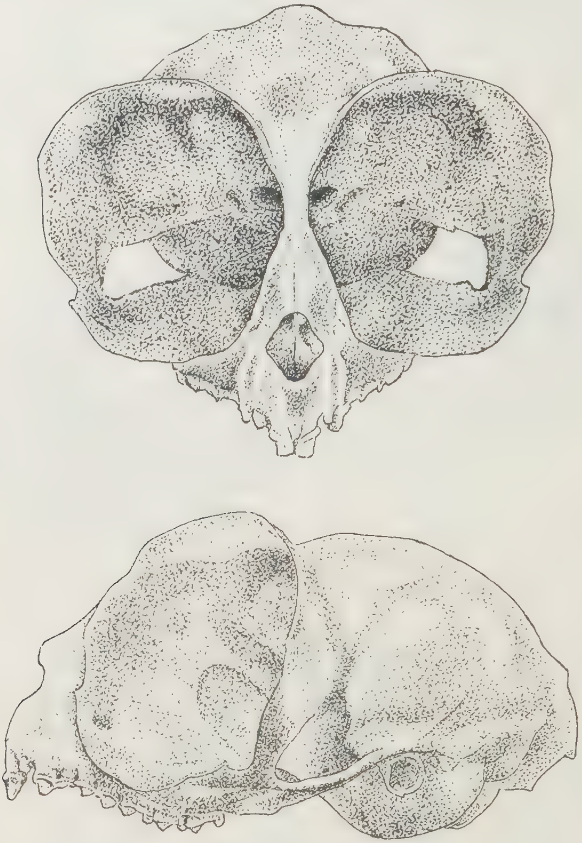

Fig. 35. *a. Tarsius tarsius* (Erxl.). Skull seen in front view. R.M.N.H. Leiden. 2.0×. Original drawing by J. E. Bevelander. *b. Tarsius tarsius* (Erxl.). Skull seen from the left side. R.M.N.H. Leiden. 2.0×. Original drawing by J. E. Bevelander.

The position of the eye ball

We shall first give the data from literature about the direction of the eye ball, next, those about the position of the eye ball in the skull.

The direction of the lateral eyes was originally far more dorsal than is found as a rule in recent Vertebrata (Franz, 1934, p. 995).

The telescope-eyes of *Opisthoproctus soleatus* Vaillant are almost parallelly directed upward, in *Argyropelecus*, in the later stages of development we also find a dorsal direction of the eyes and the eyes of the adult *Dissomma* are likewise directed upward (Franz, 1934, pp. 1049, 1050). The eyes of *Chologaster papilliferus* Forbes are directed forward and upward (Franz, 1934, p. 1052). In *Bathymaster signatus* Cope and in *Tetrabrachium ocellatum* Gthr the eyes are said to be directed upward (Gregory, 1933, pp. 358, 394). The eyes of *Platycephalus*, Gobioidei, *Uranoscopus*, *Antennarius* and allied Pediculati are said to be directed or to look partly upward (Gregory, 1933, pp. 330, 346, 365, 390). In *Laevoceratias* the eyes are directed partly upward and also outward (Gregory, 1933, p. 410). In *Myoxocephalus jaok* (C. & V.) (see my fig. 22) and allied Scorpaenoidei the eyes are directed chiefly upward (Gregory, 1933, p. 333). The statement, that in *Sternoptix* the eyes are upturned and that in *Pelor japonicum* C. & V. the eyes are turned upward, probably refers as well to the direction of the axis of the eye ball (Gregory, 1933, pp. 157, 438). – The eyes of *Rhynchoceratias* are said to have an outward direction (Gregory, 1933, p. 410). – In *Mola mola* (L.) the eyes look outward and slightly forward (Gregory, 1933, p. 295). Also in *Haplophryne hudsonius* Beebe the eyes look outward and forward (Gregory, 1933, p. 407). – The telescope-eyes of *Winteria telescopa* Brauer are parallelly directed forward (Franz, 1934, p. 1049). Also the telescope-eyes of *Stylophorus chordatus* Shaw and of *Aceratias macrorhynchus* Brauer are directed forward (Gregory, 1933, pp. 299, 407, 410). Extremely remarkable is the change in the direction of the eyes during the ontogeny of the Heterosomata.

In Aves the eyes have mainly a lateral direction, but they also look a little forward and downward; in *Scolopax rusticola* L., however, the eyes also look a little backward (Owen, 1866 II, pp. 62/63) (see my fig. 36). In Striges the eyes look forward (see my fig. 34).

In the lower Mammalia the position and consequently also the direction of the eye is rather strongly lateral, on an average, the binocular vision increases, however, with the higher development (Franz, 1934, p. 1255). Franz (1934, p. 1255) gives the following figures about the size of the angle between the eye axis and the sagittal axis of the head ("Sehachse gegen die Sagittalachse des Kopfes"): *Jaculus* (*Dipus*) 90°; Rodentia 85°

(*Lepus europaeus* Pall.) to 35°; Marsupialia 76° to 30°; Ungulata 72° to 46°; Carnivora 52° (species of the genus *Panthera*) to 5°; *Tachyglossus* (*Echidna*) 25° (on p. 1257 the eyes are said to have a somewhat lateral, half forward direction); Pteropodinae about 20° ("um 20° herum"); Lemuroidae (Prosimiae) about 10° ("um 10°") (on p. 1264 it is said that the eyes of the species of the genus *Lemur* are not directed so strictly forward as in the rest of the Lemuroidae); all Monkeys and also *Homo* 0° (*i.e.* the axes of the eyes are parallel and directed forward; see also pp. 1264, 1266). In *Rupicapra rupicapra* (L.), *Capra ibex* L. and most clearly in *Oreotragus* we find a forward rotation of the axis of the eye ("Verschiebung der Blickrichtung nach vorne") (Böker, 1935, p. 138). In Pinnipedia the eyes are placed somewhat divergently, which is often accompanied by an upward direction of the eyes (Weber, 1927 I, p. 184; Franz, 1934, p. 1255). In Cetacea the direction of the eyes is lateral, but mostly obliquely downward (Franz, 1934, p. 1255).

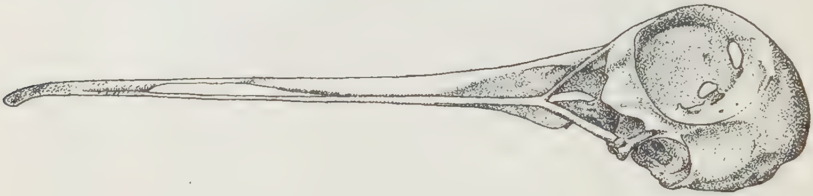

Fig. 36. *Scolopax rusticola* L. Skull seen from the left side. R.M.N.H. Leiden. 1.03×. Original drawing by G. van Gelderen.

Concerning the position of the eyes we must distinguish the position in a vertical direction (more upward or downward) and the position in the horizontal direction (more forward or backward).

Originally, the eyes lay probably completely or almost completely in the median plane, so far dorsally according to Franz (1934, p. 995).

A dorsal or upward displacement of the eyes is found among the Pisces in *Polynemus*, *Angelichthys*, *Pomacanthus* (see my fig. 24) and in the Acanthuridae and still more in the Balistidae (Gregory, 1933, pp. 268, 278, 439). In *Astroscopus y-graecum* (C.V.) (see my figs 42 and 50) the eyes have moved to the top of the skull, shifted to its dorsal surface (Gregory, 1933, pp. 367, 368, 439). Also in *Callorhynchus* the eyes have shifted in the dorsal direction (HOLMGREN & STENSIÖ, 1936, p. 335). In *Uranoscopus* the eyes lie together on the top of the head (OWEN, 1866 I, pp. 331/332). In *Luvarus* the eye lies low in the head, well below the level of the vertebral column (GREGORY, 1933, p. 306).

A far rostral position is found in the following cases. In *Sphyrna* (*Zygaena*) the eyes lie on the edges of the suddenly projecting shelves on either side of the head, the front end of which shows an extreme growth (GREGORY, 1933, pp. 101/102). In *Gymnarchus* the eye is placed far forward (GREGORY, 1933, p. 173). In *Erythrinus* the eye is placed relatively far forward (GREGORY, 1933, p. 183). A forward displacement or position shows the eye in *Gastrostomus* and in the Lyomeri in general, in *Lates niloticus* (Gmel.) (see my fig. 21), in *Polynemus* and in *Uranoscopus* (GREGORY, 1933, pp. 213, 242, 268, 365, 439/440). The eyes of *Cyclothone* are said to be pushed far forward to the front end of the interorbital bridge (GREGORY, 1933, p. 439). In *Polyodon* the eye lies above the front end of the upper jaws and in *Acipenser* as well it lies above the anterior part of the upper jaw and is said to lie relatively far forward, but in both cases the eye lies far behind the rostral point of the long rostrum (GREGORY, 1933, pp. 117, 119, figs 17, 19).

Concerning the position of the eye in the horizontal direction we can state the following.

Among Pisces, the eyes in *Pelor japonicum* C. & V. are pushed backward (GREGORY, 1933, p. 438). In Acanthuridae and still more in Balistidae the eyes have moved backward to such an extent that they actually override the hyomandibulars; orbitae, which are situated so far backward are merging the interorbital bridge with the roof of the cranial vault (GREGORY, 1933, p. 439). Also in *Angelichthys* and *Pomacanthus* the eyes are displaced backward beyond the level of the hyomandibular (GREGORY, 1933, p. 278). In *Lophius* the eyes retain their position immediately in front of the hyomandibular; the preorbital region is long (GREGORY, 1933, p. 396).

In *Homo sapiens* L. the eyes have a frontal position (BÖKER, 1935, p. 148). Also the eyes of jumping Mammalia have a frontal position or have shifted more or less to the front ("oder sind der frontalen Ebene genähert"); we find this in Carnivora, *Rupicapra rupicapra* (L.) and *Capra ibex* L., most clearly in *Oreotragus* (see my fig. 37) (BÖKER, 1935, p. 138). Also in Pinnipedia the eyes have a frontal position (Weber, 1927 I, p. 184; Franz, 1934, p. 1255).

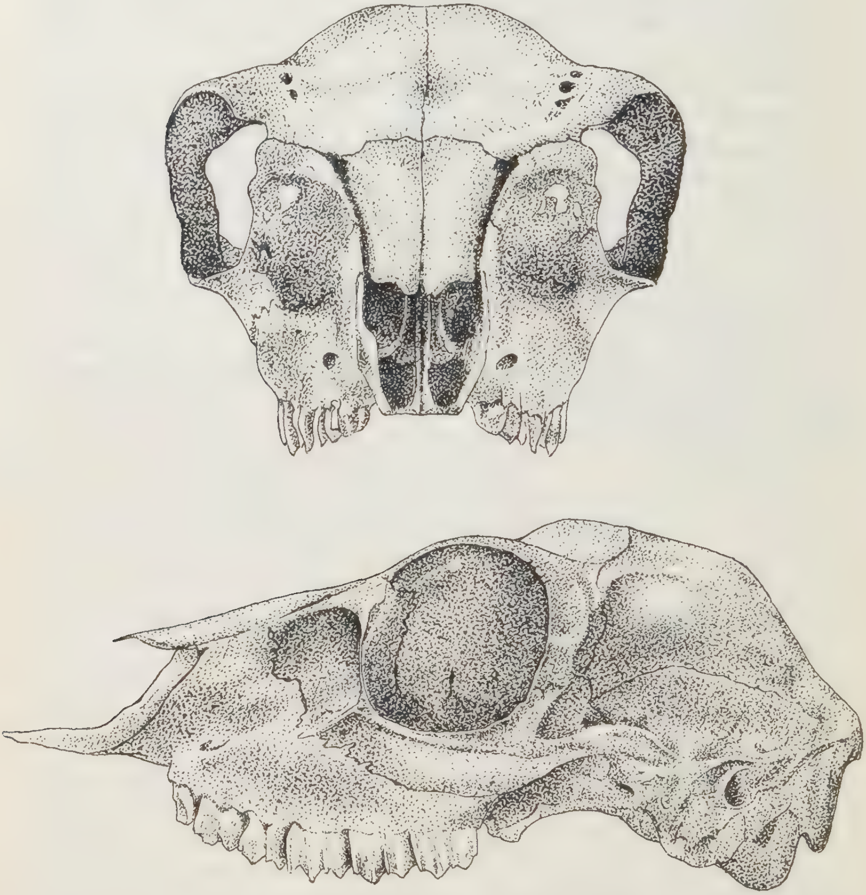

Fig. 37. *a. Oreotragus oreotragus* (Zimm.). Skull seen in front view. R.M.N.H. Leiden, Cat. C. 0.75×. Original drawing by J. E. Bevelander. *b. Oreotragus oreotragus* (Zimmı.). Skull seen from the left side. R.M.N.H. Leiden, Cat. C. 0.75×. Original drawing by J. E. Bevelander.

The position of the orbita

Data about the direction of the orbita, *i.e.*, of the axis of the orbita, are rare. Above, we have already seen, that we can only avail ourselves with some reserve of the data concerning the direction of the eye ball for designing the direction of the orbita, because the direction of these two axes is rather often divergent (see my fig. 34).

In recent skulls, both platybasic and tropidobasic skulls, the orbitae, in general, are directed laterally.

For Pisces GREGORY (1933, pp. 259, 371, 374) states, that the orbitae are directed laterally in *Trichodon*, that in *Cirrhites* the orbitae look partly upward and that in *Blennîus* the orbitae project upward.

Direct data about the position of the orbita are relatively rare as well, but for these we can also use those concerning the position of the eye ball itself.

In recent skulls, both platybasic and tropidobasic skulls, the orbitae in general lie on the side of the skull.

Originally, the orbitae lay completely or almost completely in the median level of the skull. The parietal position of the orbitae in some fossil Pisces, as † *Ateleaspis*, † *Cephalaspis* and † *Pterichthys*, and the relatively far dorsal position in † Stegocephala (see my figs 38 and 39) (FRANZ, 1934, p. 995), points to this.

A far dorsal position is also found among the recent Pisces. According to GREGORY (1933) the orbitae in *Pelor japonicum* C. & V. lie on the top of the skull, "like those of a hippopotamus" (p. 329), in the Gobioidei the orbita shows a subdorsal position (p. 346), in *Anableps tetrophthalmus* Bl. the upper borders of the enormous orbitae protrude high above the level of the cranial roof (p. 220) (see my fig. 40), in *Lactophrys* the eyes are raised, drawing the orbital roof with them (p. 286), in *Stylophorus chordatus* Shaw we find an upward arching of the interorbital bridge (p. 300), and also in *Periophthalmus* the orbitae are lifted above the rest of the skull (p. 347) (see my fig. 41). The Heterosomata show the transference of both eyes and orbitae to one side of the skull (GREGORY, 1933, pp. 344, 439).

In the aquatic Reptilia the orbitae are sometimes directed upward (see also my figs 53 and 54), as is the case in the † Nothosauria (WILLISTON, 1925, pp. 11, 247). Also in the † Ichthyopterygia the orbitae are vertical (OWEN, 1866 I, p. 158).

The following can be stated about the position in the rostrocaudal direction.

In Euselachii the position of the orbita in the skull generally varies little, according to HOLMGREN & STENSIÖ (1936, p. 312). This probably refers to, or refers as well to the position in the rostro-caudal direction. It certainly does not apply, however, to the higher Pisces, judging by the following data, mainly taken from GREGORY (1933). We may point out, that the statements concerning the position of the eye in fossils will be considered as valid for the orbita.

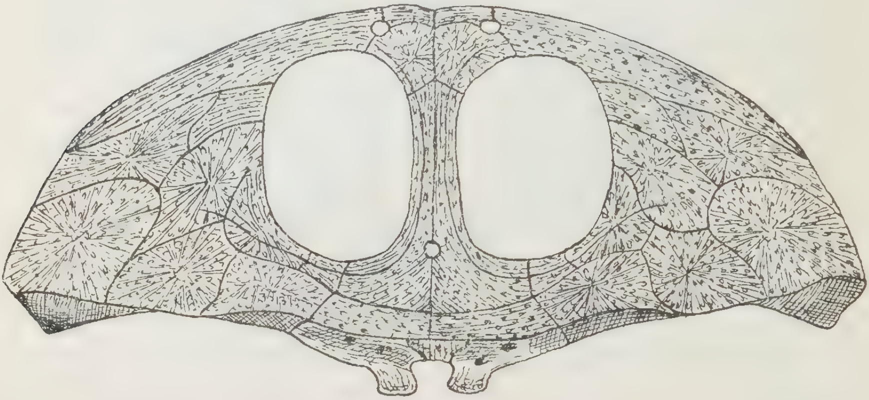

Fig. 38. *Plagiosternum granulosum* E. Fraas. Skull seen from above. After ABEL (1919), fig. 221 on p. 293.

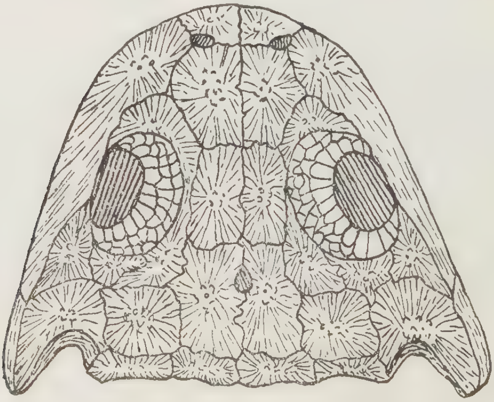

Fig. 39. *Branchiosaurus amblystomus* Credn. Skull seen from above. After STADTMÜLLER (1936) IV, fig. 385 on p. 513.

In the † Palaeoniscidae, as among others in † *Cheirolepis*, the orbitae lie far forward in the skull (GREGORY, 1933, pp. 85, 112; HOLMGREN & STENSIÖ, 1936, p. 399). In † *Cheirolepis* the orbita lies above the anterior end of the primary upper jaws (GREGORY, 1933, p. 112). In † *Acentrophorus* the orbita is located partly behind and above the very small upper jaw (GREGORY, 1933, p. 125). Also in the primitive fossil Chondrostei the orbitae are placed forwardly (GREGORY, 1933, p. 131). In † *Tomognathus mordax* Dixon as well the orbita is far forward (GREGORY, 1933, p. 157). In *Notopterus chitala* (H.B.) the orbitae have moved forward to the front of the head (GREGORY, 1933, p. 168). In *Anarhichas* the orbitae are far forward (GREGORY, 1933, p. 377). In *Astroscopus y-graecum* (C.V.) there is an extreme forward displacement of the orbitae (GREGORY, 1933, p. 369) (see my figs 42 and 50).

A backwardly positioned orbita occurs in the † Macrosemiidae (GREGORY, 1933, p. 131). In † *Furo* (*Eugnathus*) the backwardly migrated orbita lies far backward (GREGORY, 1933, pp. 131, 132). In contrast with the typical isospondylous type, the posterior border of the orbita in † *Hoplopteryx lewesiensis* (Mantell) is so far back that it nearly touches the hyomandibular (GREGORY, 1933, p. 234). In *Micropterus dolomieu* Lac. the distance between the posterior border of the orbita and the preopercular is relatively much greater than it is in † *Hoplopteryx lewesiensis* (Mantell), while in *Luciolates* this lengthening is further emphasized (GREGORY, 1933, pp. 238/239). In the Acanthuriformes (Teuthidoidei), Zanclidae and Balistidae the orbitae show a relatively posterior position (GREGORY, 1933, p. 283). In *Balistes* the posterior border of the orbitae is almost flush with the occiput and practically on top of the pterotic and hyomandibular socket, this being an advantage for a nibbling fish to have its eyes as far back as possible from the tip of the pincer-like mouth (GREGORY, 1933, p. 284) (see my fig. 43). In *Antennarius* and allied

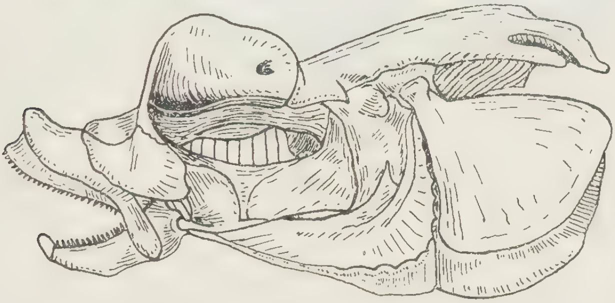

Fig. 40. *Anableps tetrophthalmus* Bl. Skull seen from the left side. After GREGORY (1933), fig. 98 on p. 220.

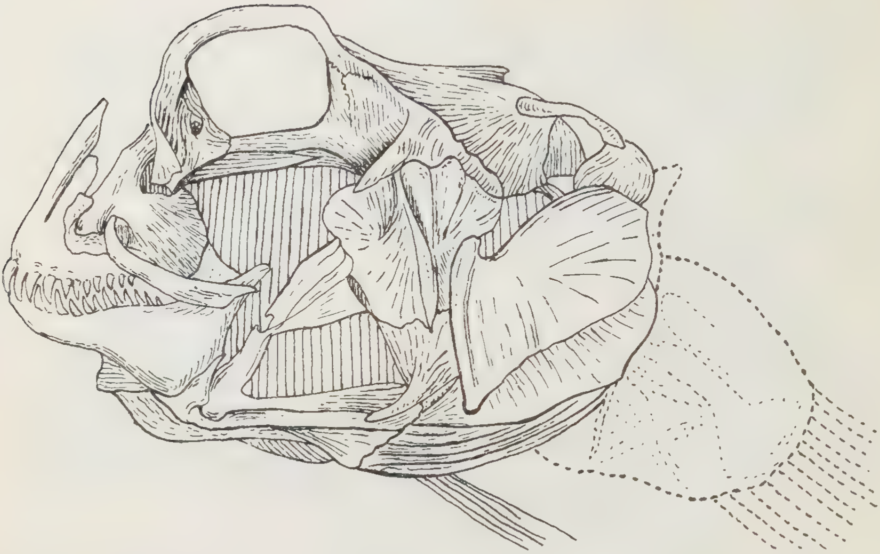

Fig. 41. *Periophthalmus*. Skull seen from the left side. After GREGORY (1933), fig. 228 on p. 347.

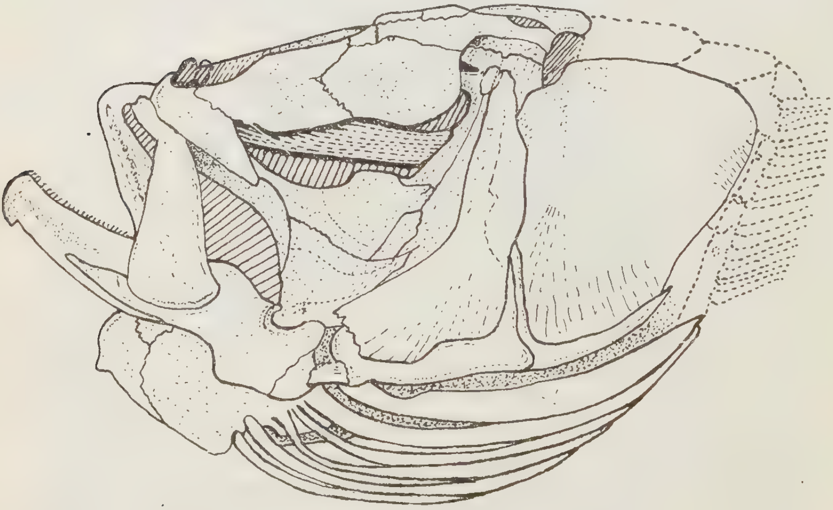

Fig. 42. *Astroscopus*. Skull seen from the left side. After GREGORY (1933), fig. 247 on p. 368.

Pediculati the orbitae are pushed backward so that they impinge upon the suspensorium (GREGORY, 1933, p. 391).

In the embryonic stages of many Teleostei the eye and also the orbita lies in close proximity of the opercular fold. This remains in the adult stages of the oldest Protospondyli (we have seen that the † Macrosemiidae were already different). In many species of higher Teleostei as the individual becomes older, the space between the orbita and the opercular flap will increase

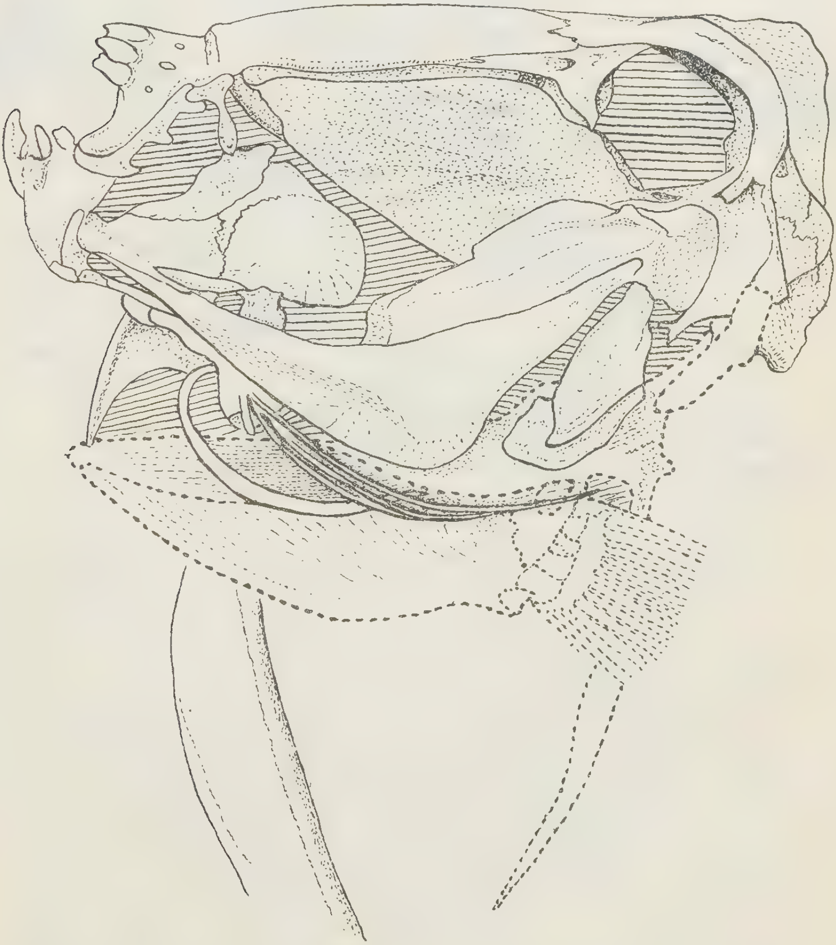

Fig. 43. *Balistes carolinensis* Gmel. Skull seen from the left side. After GREGORY (1933), fig. 161 on p. 283.

by lengthening of this space (GREGORY, 1933, p. 428, see also p. 125).

Among the Reptilia the orbitae in the † Nothosauria, as in the aquatic † Labyrinthodontia are placed far forward (WILLISTON, 1925, pp. 11, 247). In † *Ornithodesmus* (see my fig. 44) they are placed far backward, in *Chitra* (see my fig. 45) very far forward.

The orbitae of the Aves are generally placed at the sides of the skull (see my figs 33, 36, see also 13, 14 and 56); but the orbitae in the Striges (see my fig. 34) have "a more anterior aspect" (OWEN, 1866 II, pp. 62/63).

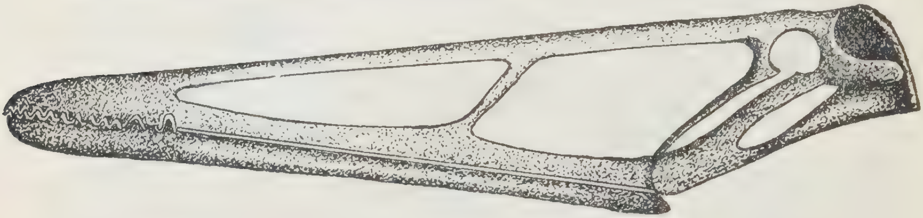

Fig. 44. *Ornithodesmus latidens* Seeley. Skull seen from the right side in mirror image. After ABEL (1919), fig. 447 on p. 570.

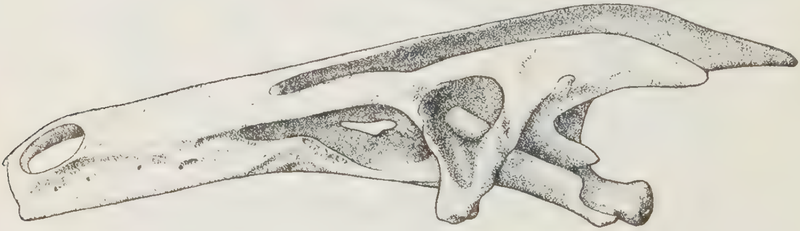

Fig. 45. *Chitra indica* (Gray) ♀. Skull seen from the left side. R.M.N.H. Leiden, no. 7054 Java. 0.5×. Original drawing by G. VAN GELDEREN.

Among the Mammalia the orbitae show an extremely lateral direction in *Jaculus* (*Dipus*), in *Daubentonia* they point obliquely forward, outward and also upward, while in *Homo*, the other Primates (see my figs 46 and 47) and also in *Phoca* (see my fig. 48) they are placed forwardly and frontally; moreover, in *Homo* and in many Monkeys the orbitae are very close together and the interorbital region is narrow (OWEN, 1866 II, pp. 511, 526, 535; WEBER, 1927 I, pp. 76, 184; KINGSLEY, 1925, p. 220; STADTMÜLLER, 1936, pp. 883, 952, 958, 988, 990). Among the Suidae, possessing large canines ("Hauer"), the eyes and consequently the orbitae lie relatively far backward in the skull and are therefore also farther apart. The distance ("Entfernung") of the occiput to the orbitae in percentages of the total skull length is in *Potamochoerus: Hylochoerus: Phacochoerus* (see my fig. 49) as 26.5 : 23 : 13.5 (Böker, 1937, p. 33).

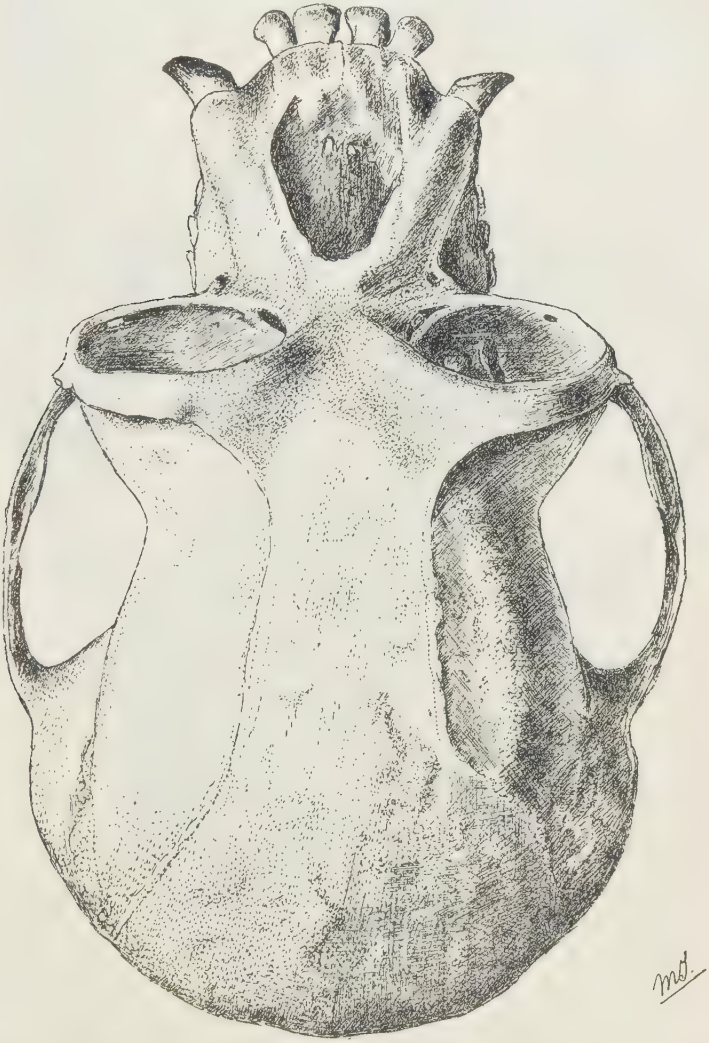

Fig. 46. *Hylobates syndactylus* (Desm.). Skull seen from above. Nat. size. Original drawing by Mrs M. Idenburg in the coll. of dr K. W. Dammerman.

It only remains for us to discuss the position of the orbita with regard to other functional components of the skull. We shall discuss the position with regard to the other orbita, with regard to the temporal region, the cerebral capsule and the nasal capsule.

In platybasic skulls there is a clear space and distance between the orbitae, in tropidobasic skulls this distance is very limited; the orbitae are sometimes separated by a skeletal septum inter-

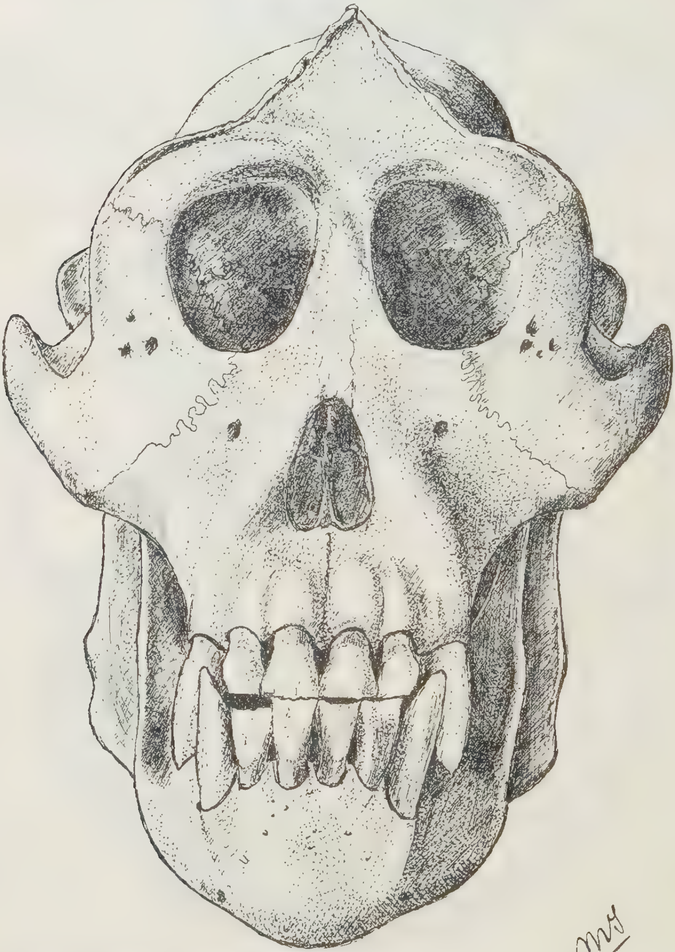

Fig. 47. *Pongo pygmaeus* (Hopp.). Skull seen in front view. 0.5×. Original drawing by Mrs M. Idenburg in the coll. of dr K. W. Dammerman.

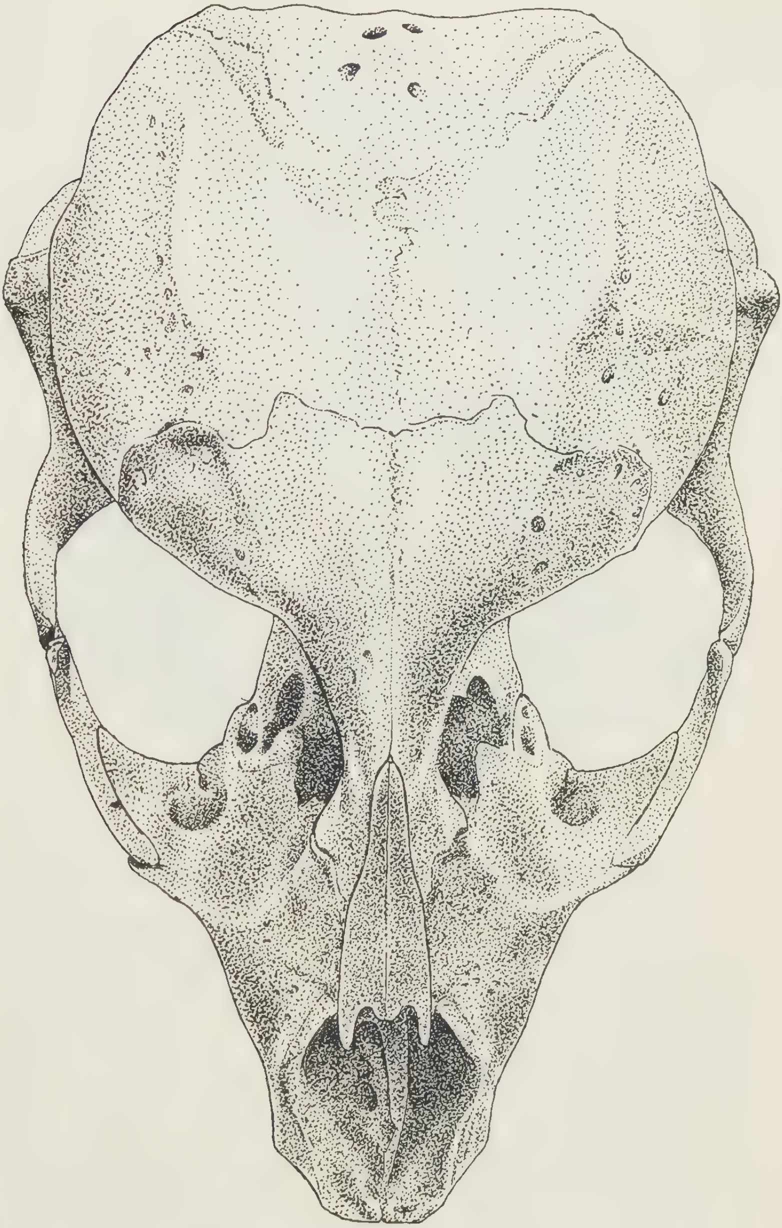

Fig. 48. *a. Phoca vitulina* L. ♀. Skull seen in dorsal view. R.M.N.H. Leiden, no. 2525. Nat. size. Original drawing by J. E. Bevelander.

orbitale, in other cases a septum of this kind is absent. In the Reptilia and Aves a skeletal septum interorbitale between the orbitae is for the greater part lacking. In the Picidae the osseous interorbital septum is very well developed, which entails an increased inflexibility ("Versteifung") of the skull (Böker, 1937, p. 30). Also in tropidobasic skulls the orbitae are dorsally separated by a more or less broad osseous roof. In Pisces its width depends on the size of the eye and on the eye having a more or less pronounced dorsal direction. Thus, the interorbital bridge in the Chimaeroidea, in *Stylophorus chordatus* Shaw, *Opisthoproctus* and *Periophthalmus* shows a marked constriction and in *Astroscopus* (see my fig. 50) it is very narrow, in every case connected with the large or enormous size of the orbitae, while in the Mormyridae the interorbital bridge is broad, due to the reduction of the eye (Gregory, 1933, pp. 103, 300, 439). The latter is also the case in *Lepisosteus* (see my fig. 51). The difference in breadth of the interorbital bridge in different races of *Anas platyrhyncha* L. has another cause; it is apparently due to the different development of the nasal gland (Stresemann, 1927, pp. 52, 122) (see my fig. 52). In the Suidae, possessing large canines ("Hauer"),

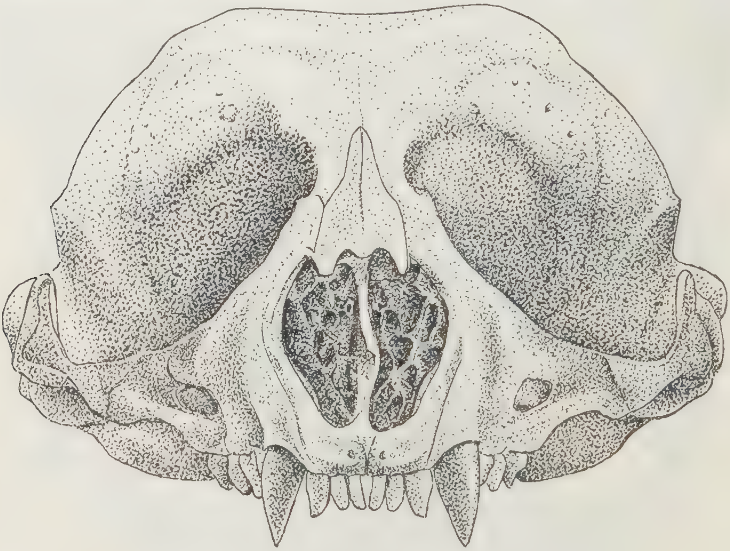

Fig. 48. *b. Phoca vitulina* L. ♀. Skull seen in front view. R.M.N.H. Leiden, no. 2525. Nat. size. Original drawing by J. E. Bevelander.

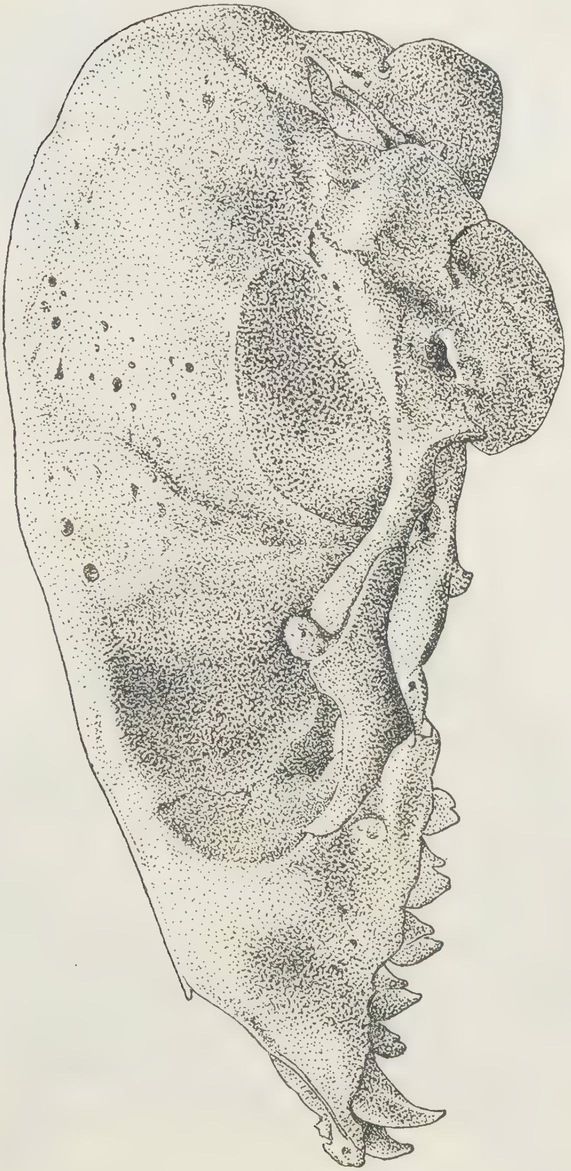

Fig. 48. *c. Phoca vitulina* L. ♀. Skull seen from the left side. R.M.N.H. Leiden, no. 2525. Nat. size. Original drawing by J. E. Bevelander.

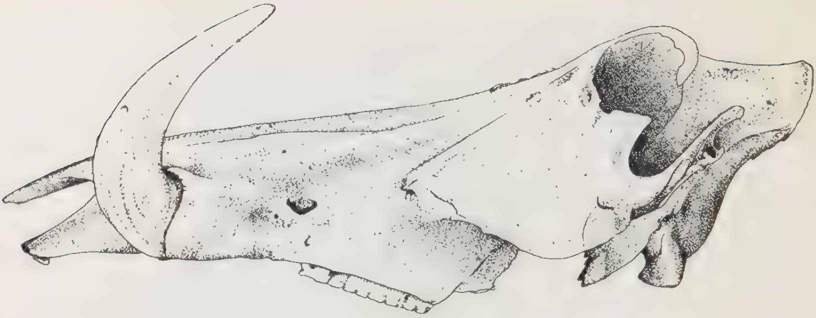

Fig. 49. *Phacochoerus aethiopicus* Pall. ♂ ad. Skull seen from the left side. R.M.N.H. Leiden, no. 812. Putzy East Africa. 0.27×. Original drawing by G. van Gelderen.

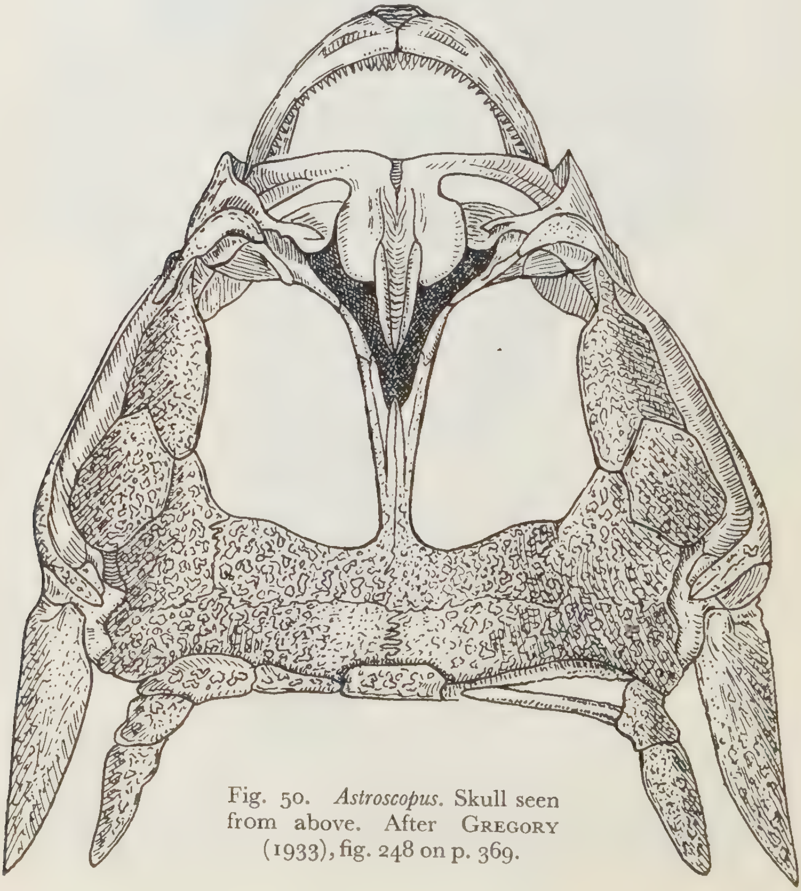

Fig. 50. *Astroscopus*. Skull seen from above. After Gregory (1933), fig. 248 on p. 369.

the orbitae lie far backward in the skull; the connecting line of the eye, and consequently also of the orbita, in percentages of the total skull length is in *Potamochoerus: Hylochoerus: Phacochoerus aethiopicus* Pall. as 28.5 : 31 : 42 (BÖKER, 1933, p. 33).

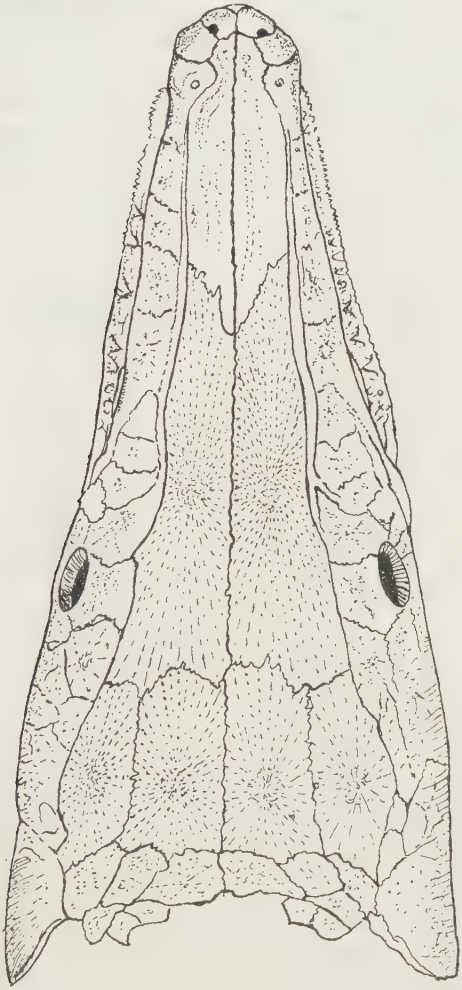

Fig. 51. *Lepisosteus tristoechus* (Bl. Schn.). Skull seen from above. After GREGORY (1933), fig. 23 A on p. 128.

In determining the position of the orbita with regard to functional components in the temporal region of the skull, we are also concerned with the position of the orbita with regard

4. NASAL CAPSULE

a. Introduction

We understand by the nasal capsule the cavity in the skull, in which the organ of smell with its olfactory and its respiratory part and its auxiliary organs is situated, together with the thin layer of cartilage or bone lining this cavity.

The skeletal wall of the nasal capsule is not appreciably extra thickened – except in some cases locally, where bony processes occur on the "nose" – so that the outer wall of the skeletal nasal capsule supplies us with a not incorrect index for the size and the form of the nasal capsule.

b. The connection between the size and the shape of the nasal capsule and the size and the shape of the olfactory organ

The size and the form of the skeletal nasal capsule is very closely connected with the development of the organ of smell in its olfactory and respiratory part. Nowhere in literature have I come across any statements that the size and form of the nasal capsule should not be determined by those of the soft organ of smell; nor have I found anything about voluminous organs which lie in the skeletal nasal capsule, with the exception of the olfactory organ.

c. The size and the shape of the olfactory organ

In the now following discussion about the size and the form of the olfactory organ we shall not consider the so-called accessory nasal sacs, which occur in many Teleostei, and the sinus pneumatici, which occur in Loricata (Crocodilia), Aves and Mammalia; they are immaterial to the olfactory organ itself, at least in the Mammalia (MATTHES, 1934, pp. 888, 890, 919, 924, 926, 934).

The data in literature about the size of the olfactory organ are such, that to distinguish between data about an absolute and a relative size of the olfactory organ is impossible. It is practically certain that all data refer to a relative size of the olfactory organ.

In stages of development

In the determination of the relative size of the olfactory organ the age of the animal must be taken into account. Thus, in the ontogeny of the Mammalia the size relation between the nasal capsule and consequently therefore also the olfactory organ, and the cerebral capsule is more and more shifted in favour of the nasal capsule (MATTHES, 1934, p. 928).

In adult animals

In Pisces the olfactory fossae are relatively small sacs (MATTHES, 1934, p. 888). In Dipneusta (Dipnoi), however, the olfactory organs are conspicuously protracted (MATTHES, 1934, p. 892). In Chondrostei the external nostril has a far frontal position on the long rostrum, while the nasal capsules lie at the basis of the rostrum (KINGSLEY, 1925, p. 99; see however MATTHES, 1934, fig. 680), pointing, in my opinion, to a protracted form. The same may be the case in *Lepisosteus*, where the two pairs of external nostrils lie very far forward on the very long secondary rostrum (MATTHES, 1934, pp. 891/892). GREGORY's extensive study (1933) contains a number of data about the nasal sacs, olfactory sacs, nasal chambers, olfactory chambers and olfactory fossae, which probably do not refer to the skeletal nasal capsule, but to the soft olfactory organ. They may therefore be quoted here. *Rhynchobdella aculeata* (Bloch) shows hypertrophied olfactory chambers (GREGORY, 1933, p. 353). *Aceratias* shows great growth of the nasal sacs, while in *Haplophryne hudsonius* Beebe the olfactory sacs are not so well developed as those of *Aceratias* (GREGORY, 1933, pp. 407, 410). *Mastacembelus* has large nasal chambers (pp. 353/354). In *Percopsis guttatus* Ag. the olfactory fossa is relatively large (p. 232). In *Crapatalus* the nasal chamber is less reduced than in *Uranoscopus* (p. 365). In *Laevoceratias* the olfactory sacs are reduced (p. 410). In *Astroscopus* the olfactory chambers are very small; the constriction of the olfactory chamber is primarily due to the small size of the enclosed sensory capsule (p. 369). From this last datum it might be inferred that GREGORY with "olfactory chamber" means the skeletal nasal capsule and not the soft olfactory organ.

In the Amphibia we find in stead of the nasal fossa of the Pisces a more strongly developed nasal cavity, owing to which the primordial neurocranium of the Amphibia has a strongly developed regio ethmoidalis (STADTMÜLLER, 1936, p. 514). A comparison between Pisces and Amphibia shows a certain preponderance of the indifferent epithelium over the olfactory epithelium, in the latter, but in *Triturus* (*Triton*) and *Bufo* the olfactory epithelium still covers a much greater surface than the indifferent epithelium (MATTHES, 1934, figs 683, 695, 696). The indifferent epithelium in Amphibia serves as respiratory epithelium and is found in the atrium s. vestibulum, generally present in Amphibia, and further in the olfactory cavity proper, although rarely as a separate respiratory passage; at the utmost it constitutes a groove in the olfactory cavity proper (MATTHES, 1934, pp. 894, 898, 906). In cross section the olfactory cavity of the Amphibia has its greatest extension in transverse or oblique direction (MATTHES, 1934, p. 907).

In the Amniota the nasal cavity is relatively much larger, which is due to the development of the respiratory passage as a passage clearly separated from the coecal pars olfactoria; this is a direct and wide passage from the external nostril to the choana (MATTHES, 1934, p. 906). The difference in size between the nasal cavity in the various classes of the Vertebrata and also within each of these classes is therefore not so much dependent on the size of the pars olfactoria. Of course there are differences in size, but a higher developed olfactory organ is yet principally characterized by the development of olfactory folds in the Pisces and of conchae ("Muscheln") in the Amniota, which occasion an enlargement of the surface, without the pars olfactoria as a whole increasing much in size.

In the Reptilia the nasal cavity is or can be very well developed (STADTMÜLLER, 1936, p. 919). In cross section the pars olfactoria is longest in the vertical direction (MATTHES, 1934, p. 907). Compared with the Amphibia the nasal cavity of the Reptilia has extended in orocaudal direction, in accordance with the development of the whole preorbital region of the head of the Reptilia (MATTHES, 1934, pp. 907, 908). This is most strongly the case in the Loricata (Crocodilia), where the non-olfactory front part of the nasal cavity is very much protracted and occupies more than half of the complete olfactory organ; in cross section this part is broad and flat (MATTHES, 1934, pp. 907, 918/919). In the Testudines (Chelonia) the nasal cavity is much shorter, in accordance with the form of the skull, but also higher than in other Reptilia; in cross section it is a vertical oval ("hochgestelltes Oval") (MATTHES, 1934, p. 915). In the Serpentes (Ophidia) the atrium s. vestibulum is very incompletely developed; the aquatic snakes (Hydrophidae, Acrochordidae, Homalopsidae), where the atrium is very well developed in connection with the formation of a closing-mechanism, are exceptions to this rule (Matthes, 1934, pp. 908, 914). The size of the atrium s. vestibulum does not always procure a measure for the length of the nasal cavity in longitudinal direction, because the atrium is not always placed rostrally of the pars olfactoria; among the Sauria (Lacertilia) there are groups in which the atrium lies partly beside the main cavity, in other groups it lies partly dorsally of the main cavity (Matthes, 1934, pp. 908, 909/910). Its position is influenced by the room available in this part of the head and the position of the external nostril (Matthes, 1934, p. 908).

In the Aves the nasal cavity in general is small, though it is relatively well developed both in longitudinal and in dorsoventral direction, compared to the development in transverse direction (Matthes, 1934, pp. 922, 926). The Tubinares, and especially *Apteryx*, with a very well developed olfactory organ are an exception (Haller von Hallerstein, 1934, pp. 168/169; Matthes, 1934, p. 924; Marinelli, 1936, p. 821).

Among all Vertebrata, the nasal cavity is relatively most voluminous in the Mammalia; it occupies about the front half of the skull, which is more than in all lower Vertebrata, the Loricata (Crocodilia) excepted (Matthes, 1934, pp. 926, 928). The pars olfactoria occupies a proportionally small part of the space of the complete nasal cavity of the Mammalia (Matthes, 1934, p. 926). Compared with the Non-Mammalia the olfactory cavity of the Mammalia is more extended in a caudal direction, owing to the very well developed pars ethmoturbinalis, which extends far in the caudal direction (Matthes, 1934, p. 928). The development of the pars olfactoria is naturally also connected with the fact whether the Mammalia concerned are anosmatic (Odontoceti), almost anosmatic (Mystacoceti), microsmatic (*Ornithorhynchus*, Sirenia, Pinnipedia, Primates), or macrosmatic (most of the remaining Mammalia) (Haller von Hallerstein, 1934, pp. 176, 178, 183; Matthes, 1934, pp. 934, 938, 940, 942).

We may add some data about the size of the complete nasal cavity in Mammalia. In many Rodentia the nasal cavity is larger than the cranial cavity for the brain (Weber, 1927 I, p. 209; Stadtmüller, 1936, p. 919). Owen (1866 II, p. 535) states that in *Pongo pygmaeus* (Hopp.) the area of the nasal cavity equals more than one third of that of the cranial cavity. For the rest we meet with an increasing reduction of the olfactory organ in the Primates, from the Lemuroidae (Prosimiae) up to *Homo* (Stadtmüller, 1936, pp. 989, 990, 992), although, according to Matthes (1934, p. 938) *Homo* is far from having the worst developed olfactory organ among the Primates. In the Marsupialia there is a great extension of the nasal cavity (Owen, 1866 II, p. 335).

d. The size and the shape of the nasal capsule

Several facts about the size and form of the nasal capsule can be deduced indirectly from data about the size and form of the olfactory organ, as we mentioned above.

In stages of development

Above we have seen already that in the ontogeny of the Mammalia the proportion between the size of the nasal capsule and the cerebral capsule is more and more shifted in favour of the nasal capsule (Matthes, 1934, p. 928).

In adult animals

Direct data about the size of the nasal capsule in Non-Mammalia are rare in literature.

Concerning Pisces we may first of all recall to mind, that we collected and quoted above a number of statements from Gregory (1933), about the size of the nasal sacs, olfactory sacs, nasal chambers, olfactory chambers and olfactory fossae, which may partly refer to the skeletal nasal capsule as well. Besides, we find in Gregory (1933) the following data: in *Coryphaena* there is a large osseous nasal cavity (p. 305), in *Aceratias macrorhynchus* Brauer the olfactory capsule is great (p. 407), in Euselachii the olfactory capsules are very varied, possibly as to size as well (p. 440), whereas in the Teleostei it usually shows a great reduction (p. 440), also the neurocranium of a Carboniferous Palaeoniscid shows a very small olfactory capsule (Gregory, 1933, fig. 13 B).

In Mammalia, the back part of the nasal capsule is widened, the front part is drawn out long and narrow, and there is also an extension in the caudal direction (Stadtmüller, 1936, p. 892). For in the Mammalia, in contrast to the Reptilia, the nasal capsule does not reach back to the processus maxillaris posterior;

the caudal third part with the recessus cupularis has been newly acquired by the Mammalia; owing to this caudal expansion, part of the septum interorbitale is taken up in the septum nasi, sometimes to a greater, sometimes to a less extent, as in Platyrrhina with their reduced nasal capsules (STADTMÜLLER, 1936, p. 898). According to MATTHES (1934, p. 928), the caudal extension to the cranial cavity for the brain (which is characteristic for the Mammalia) is attended by a well developed pars ethmoturbinalis. In Primates with a frontal position of the orbitae on either side of the median plane, the back part of the nasal capsule is narrowed; the small size of the interorbital space ("Interorbitalbreite") is secondary (KINGSLEY, 1925, p. 220; MATTHES, 1934, p. 938; STADTMÜLLER, 1936, pp. 883, 956). It is not only in the Primates, however, that we find a reduction of the nasal capsule, but also in Cetacea – especially in the Odontoceti –, in Sirenia and in the aquatic Pinnipedia (STADTMÜLLER, 1936, p. 905). Also in the Chiroptera the nasal capsule is reduced (STADTMÜLLER, 1936, p. 971).

Skull elements, surrounding the nasal capsule, may also give an indication for the size of the nasal capsule.

In the Teleostei, according to GREGORY (1933, p. 440), the olfactory capsule, be it large or small, is protected by the nasals and the lateral ethmoid. For *Astroscopus* GREGORY (1933, p. 369) states that the very small olfactory chambers are squeezed in between the articular processes of the maxillae and the forwardly displaced flanges of the lateral ethmoids.

In Mammalia the nasal capsule is surrounded by ethmoid, frontalia, nasalia, lacrimalia, maxillaria, palatina; sometimes the pterygoid contributes to the rim of the choane and the intermaxillare to the external nostril (STADTMÜLLER, 1936, p. 920).

e. The position

Here too we will distinguish between the position of the olfactory organ with the external nostril in the soft parts of the head, and the position of the skeletal nasal capsule with the skeletal external nostril in the skull.

The difference between the position of the olfactory organ and of the skeletal nasal capsule is most striking for the position of the external nostril in the soft parts of the head and the skeletal external nostril in the skull in proboscidean Mammalia. We shall see below that in a number of proboscidean Mammalia the skeletal external nostril lies at a clear distance behind the front tip of the snout, while the external nostril at the end of the soft proboscis sometimes lies very far in front of it.

The position of the olfactory organ

We will discuss the position of the olfactory organ with regard to the snout, rostrum or upper jaw and after that with regard to the cranial cavity for the brain.

Concerning the position of the olfactory organ with regard to rostrum, snout or upper jaw, we can state the following.

Among Pisces, in recent Selachii, the olfactory fossae lie on the ventral side of the rostrum between the tip of the rostrum and the transverse mouth fissure; an exception to this is *Chlamydoselachus*, where the olfactory fossae have a dorsal position on the head, but in this genus the rostrum is lacking and the mouth opening is terminal (Matthes, 1934, p. 886). In the Dipneusta (Dipnoi) the olfactory fossae are ventral, in contrast with those of the Teleostei (Matthes, 1934, p. 892). In the Teleostei the olfactory fossae lie on the dorsal side of the head, about halfway between the front tip of the rostrum and the eyes (Matthes, 1934, p. 888). In most Teleostei two separate external nostrils are found, as a rule (Matthes, 1934, pp. 888, 890; Holmgren & Stensiö, 1936, pp. 348, 427, 461).

The following data do not deal with the position of the olfactory organ as a whole, but only with the position of the external nostril in the Pisces. In Chondrostei the nostril has a very forward position on the long rostrum, according to Kingsley (1925, p. 99) (see however Matthes, 1934, fig. 680). In *Lepisosteus* the two pairs of external nostrils lie very forward on the very long secondary rostrum (Matthes, 1934, pp. 891/892).

Among the Amphibia, the external nostrils in the soft parts of the head are placed terminally and sometimes a little ventrally in the Ichthyoidea; in the Salamandridae they have a more dorsal position (Matthes, 1934, p. 896).

As we shall see later in the Reptilia the skeletal external nostril, – and also the external nostril in the soft parts of the head –, has sometimes a terminal position, once or twice it is displaced in a ventral direction and in a great number of cases dorsally, namely at the basis of the snout, close to the orbitae. This may point to a short rostro-caudal development of the nasal cavity, but it need not always be the case. For in *Monitor*, according to MATTHES (1934, p. 910) the external nostrils lie right in front of the eyes, while the atrium s. vestibulum constituting a canal, first runs forward to the neighbourhood of the snout tip and then bends backwards. According to a written information of Dr L. D. BRONGERSMA (Rijksmuseum van Natuurlijke Historie, Leiden) the external nostrils do not have such a far backward position in all species of the genus *Varanus*. In the aquatic snakes of the groups of the Hydrophidae, Acrochordidae and Homalopsidae, the external nostrils are often placed on the dorsal side of the snout, according to MATTHES (1934, p. 914). In the Sauria the nostrils always lie on the sides of the head, the distance to the snout tip and the eyes strongly varying (MATTHES, 1934, p. 910).

In Aves, the external nostrils in the "soft" parts (here the horn bill), usually lie at the basis of the upper bill. It is an exception when they lie further forward, as in the Tubinares (see my fig. 56), where the external nostrils are found on the end of tubular lengthenings, and in *Apteryx*, where the nostrils are placed subterminally, close to the tip of the bill (OWEN, 1866 II, pp. 64, 130, 131; STRESEMANN, 1927, p. 123; 1933, pp. 748, 751; 1934, pp. 790/791; MATTHES, 1934, p. 922; MARINELLI, 1936, p. 821).

In Mammalia the nasal cavity, as a rule, extends as far forward as the upper jaw, so that the external nostril is placed on the tip of the snout. In *Zeuglodon* and the Mystacoceti the external nostrils lie about the middle of the snout; in the Odontoceti (see my fig. 59) the joined nostrils lie at the basis of the snout, so they are shifted further towards the crown of the skull (KINGSLEY, 1925, p. 211; MATTHES, 1934, pp. 940, 941). In other Mammalia the nasal cavity is extended very far rostralwards, sometimes even into a long trunk. The influence of a proboscis formation on the position of the osseous external nostril will be discussed later on.

There is a great deal to be said about the position of the olfactory organ with regard to the brain and consequently to the cranial cavity for the brain, but this is best done in the discussion of the position of the nasal capsule with regard to the cerebral capsule. As we shall see it is greatly influenced by the place of exit of the nervus olfactorius and the manner in which the latter leaves the cerebral capsule to enter the olfactory organ.

The position of the nasal capsule

We will discuss the position of the nasal capsule and of the skeletal external nostril with regard to the rostrum, the snout and the upper jaw, further in relation to the cerebral capsule and finally with regard to the orbitae.

In the Elasmobranchii the position with regard to rostrum and upper jaw is such, that the nasal capsules lie in the region of the rostrum, usually at a fixed place with respect to the processus antorbitalis, but in some cases at a greater distance (HOLMGREN & STENSIÖ, 1936, p. 312). According to GREGORY (1933, p. 440) the variations in the olfactory capsules in Euselachii play an important part in modifying the fore part of the skull, which is certainly also partly due to the variations in the position. In *Sphyrna* (*Zygaena*) the olfactory capsules are pushed out to the edges of the suddenly projecting shelves on either side of the head by the extreme growth of the front end of the head with its extreme depression and widening of the rostrum (GREGORY, 1933, pp. 101/102). In most Arthrodira the nostrils have a terminal position, but in the Stegoselachii the position is dorsal between the front parts of the orbitae (HOLMGREN & STENSIÖ, 1936, p. 326). As the skull in the Teleostei lies very close under the skin the data about the position of the external nostrils in the soft parts are in general valid as well for the position of the skeletal external nostrils.

In the terrestrial Amniota the nasal capsule stretches along and above the skeletal upper jaw, so that the longitudinal axes are about parallel. The nasal capsule may stretch more or less far forward on the skeletal upper jaw.

In † Stegocephala (see my figs 38 and 39) and Amphibia (see my fig. 31) the skeletal external nostrils occupy a far forward position.

In the Reptilia the skeletal external nostrils originally lie on or near the front tip of the snout (WILLISTON, 1925, p. 10). In the Typhlopidae, a group of burrowing Serpentes (Ophidia), the external nostrils have shifted to a more ventral position (VERSLUYS, 1936, p. 786). In a great number of Reptilia the external nostrils have shifted dorsally at the basis of the snout, close to the orbitae. This is the case in most aquatic Reptilia, such as † Ichthyosauria, † Mesosauria, † Plesiosauria, † Phytosauria (see my fig. 53), † Thalattosauria, *etc.* (OWEN, 1866 I, pp. 158, 159; WILLISTON, 1925, pp. 10, 79, 81, 248, 253, 255, 264, 283, 286; Versluys, 1936, pp. 788, 797, 798). On the other hand, the external nostrils in Loricata (Crocodilia) (see my figs 10 and 54) and Choristodera lie near or on the tip of the snout (Williston, 1925, p. 10). In the † Pterosauria, according to Williston (1925, pp. 10, 296), the external nostrils are placed far from the tip of the snout, as in Aves; according to Owen (1866 I, p. 161), they are placed about halfway between the orbitae and the muzzle. In the † Diplodocidae the nostrils lie near the top of the skull, at a distance from the tip of the snout, while in † Ornithopoda their position is near the tip of the snout (Williston, 1925, pp. 293, 294).

However far forward the external skeletal nostrils in the Reptilia may be situated, the tip of the snout extends farther forward still. An exception we see in *Tetronyx*; the premaxillary part of the facial profile is not vertical, as in many Testudines (Chelonia) (see my figs 11 and 45), it runs downward and backward as well from the nostril, "the

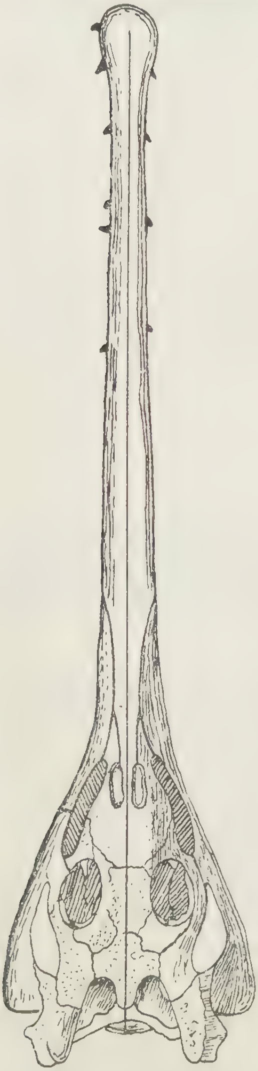

Fig. 53. *Mystriosuchus*. Skull seen from above. After Williston (1925), fig. 67 on p. 82.

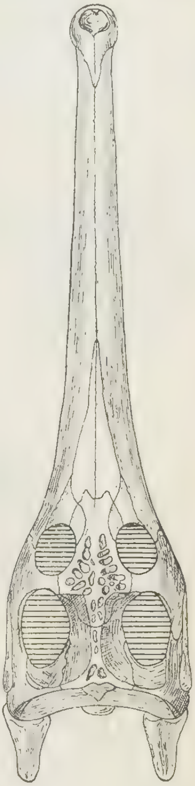

Fig. 54. *Teleosaurus*. Skull seen from above. 0.10×. After Williston (1925), fig. 68 A on p. 84.

reverse of prognathism", says Owen (1866 I, p. 130). – The situation is quite different in some † Trachodontidae; here praemaxillaria and nasalia form a very long, far projecting osseous tube for the very much lengthened nasal passage, resp. accessory cavities of the nasal cavity (see my fig. 55). In other species, however, we only find a smaller helmet, or even only a combformed helmet (Versluys, 1936, p. 795).

The literature has not enlightened me on the position of the external skeletal nostril with regard to the bone in the upper bill in Aves (see my fig. 52). In Tubinares (see my fig. 56) it lies halfway the length of the bony upper bill, in *Apteryx* (see my fig. 57) at its tip.

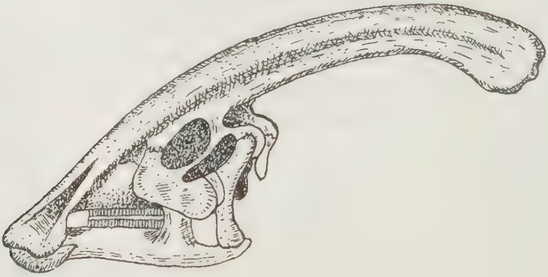

Fig. 55. *Parasaurolophus.* Skull seen from the right side in mirror image. After Versluys (1936), IV, fig. 614 on p. 795.

In the Mammalia the skeletal external nostril as a rule lies at a short distance from the front tip of the upper jaw (see my fig. 58, also my figs 2, 3, 6, 7, 8, 26, 35, 37, 48 and 49). In those cases the nasale usually varies along with the length of the snout (Kingsley, 1925, p. 195). In two categories among the Mammalia the skeletal external nostril is placed relatively far backward with regard to the front tip of the upper jaw. This is the case in those forms whose external nostril in the soft parts of the head also lies far backward, as in Cetacea, but it is also the case in proboscidean Mammalia, whose external nostril in the soft parts, on the contrary, is situated very far in front of the front tip of the upper jaw. We have seen above, that in the Cetacea the external nostrils in the soft parts of the head have shifted on the upper jaw in the direction of the orbitae. The position of the skeletal external nostril corresponds with this. In the Odontoceti the reduced nasalia are placed vertically at the caudal border of the skeletal external nostril (Kingsley, 1925, p. 212). Stadt-

Müller (1936, p. 956) remarks that the structure of the skull is largely dependent on the extension of the nasal skeleton, pointing to the fact that reduction of the nasal skeleton produces considerable diminishing ("starke Einbusse") of the facial skeleton, conspicuous in Cetacea. In my opinion, however, his remark does not bear upon the length of the snout, but probably on its height; for in Cetacea (see my fig. 59), in connection with the slight height of the snout, the cerebral skull does not pass gradually, but rather suddenly, into the facial skull, as we also observe in Aves. It is not the nasal capsule, but more the upper jaw which determines the size and especially the length of the facial skull.

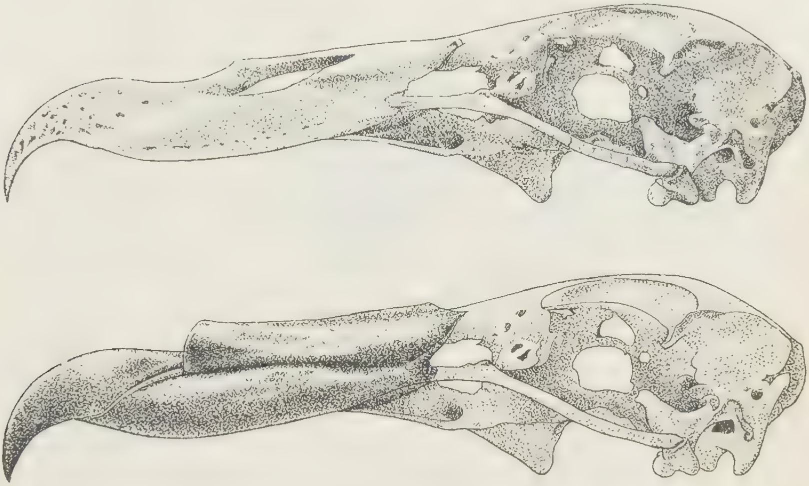

Fig. 56. Lower figure *Macronectes giganteus* (Gn.). Skull with horn-wrapping, seen from the left side. R.M.N.H. Leiden. 0.59×. Original drawing by J. E. Bevelander. Upper figure *Macronectes giganteus* (Gn.). Skull without horn-wrapping, seen from the left side. R.M.N.H. Leiden. 0.59×. Original drawing by J. E. Bevelander.

The influence of the formation of a proboscis on the position of the osseous external nostril and on the size of the nasalia is very different in various Mammalia; *Tapirus* (see my fig. 60) has prominent nasalia; *Elephas*, *Macrauchenia*, proboscidean Pinnipedia (as *Cystophora* and *Mirounga* (*Macrorhinus*)) and *Nasalis* have reduced nasalia (Weber, 1927 I, p. 220; Stadtmüller, 1936, p. 922). According to STADTMÜLLER (1936, p. 978), the caudal displacement of the external skeletal nostrils in the Proboscidea (see my figs 1 and 4) should be attributed to the development of the tusks. According to STADTMÜLLER (1936, p. 905), the formation of an external nose in Mammalia (*Tachyglossus* excepted) is dependent on the reduction of the prenasal process of the praemaxillare.

Both a strongly reduced nasal cavity and nasal capsule, and, in a number of cases the formation of a proboscis as well, leads to a dorsal and aboral shifting of the skeletal external nostrils, as is found in the Proboscidea, the Cetacea, the Sirenia and *Macrauchenia* (OWEN, 1866 II, pp. 280, 281, 440/441; FLOWER & LYDEKKER, 1891, p. 66; KINGSLEY, 1925, p. 195; STADTMÜLLER, 1936, pp. 920, 927, 987).

We must add to this, that in Mammalia in front of the osseous external nostril, formed by nasalia and intermaxillaria, often cartilaginous elements are found, which are sometimes ossified and have been called os nasi and os praenasale (STADTMÜLLER, 1936, p. 922). In proboscidean Mammalia we always find cartilage or bone in the trunk, except in *Elephas* and *Tapirus* (MATTHES, 1934, p. 939).

The position of the nasal capsule with regard to the cerebral capsule is in the first place determined by the size and the position, inclusive the incline, of the plane of the fenestrae olfactoriae and secondly by the incline of the upper jaw with regard to the cerebral capsule.

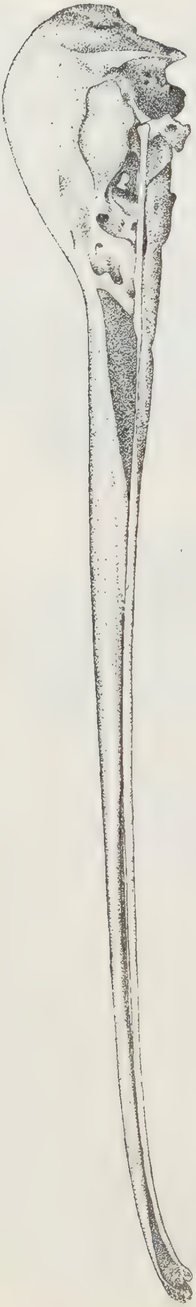

Fig. 57. *Apteryx mantelli* Barth. ♀. R.M.N.H. Leiden, no. 5705. Wellington N. Zealand from Rott. Dierg. 0.89×. Original drawing by G. VAN GELDEREN.

The size and the position, inclusive the incline, of the plane of the fenestrae olfactoriae is connected with the place and the way in which the nervus olfactorius or the fila olfactoria leave the cranial cavity for the brain to enter the nasal cavity.

Among the primitive platybasic skulls, the nasal capsules in the Elasmobranchii are placed on either side of the oral end of the cavum cranii.

In the primitive platybasic Amphibia the mutual position of nasal capsule and cerebral capsule is rather varied (STADTMÜLLER, 1936, pp. 516, 521, 546, 549, 560, 561). Originally the nasal capsules are placed laterally from the oral end of the cavum cranii. This situation subsists only in a number of Perennibranchiata and Ichthyoda. In lower Salamandridae a solid septum internasale occurs, but in all others there is a cavum internasale. Originally the brain extends into this cavum internasale; this remains in the said Perennibranchiata and Ichthyoda. But in all others the brain retreats, so that the position of the nasal capsules with regard to the cranial cavity for the brain is altered. Very often the brain case is separated from the cavum internasale by a partition of connective tissue or a carti-

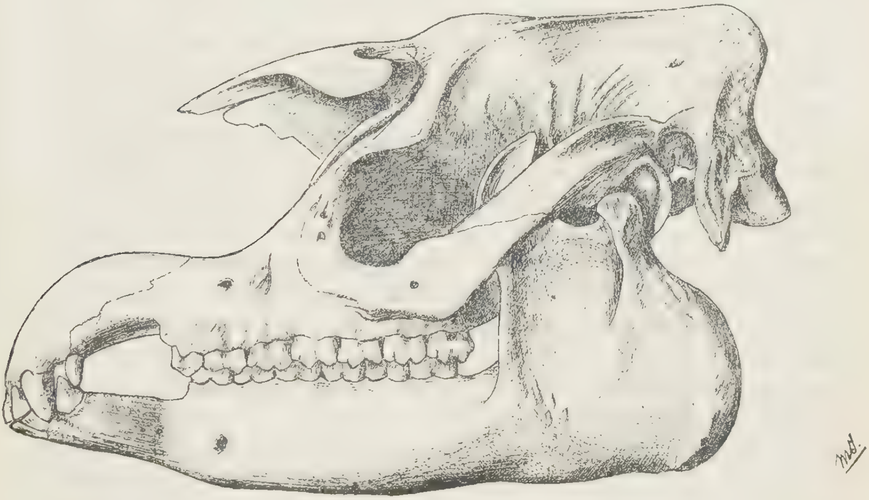

Fig. 60. *Tapirus indicus* Desm. Skull seen from the left side. 0.24×. Original drawing by Mrs M. IDENBURG in the collection of dr K. W. DAMMERMAN.

laginous septum, the septum s. planum praecerebrale, with the result that the connecting opening, the fenestra praecerebralis, is closed.

In the Sauropsida there is but one fenestra olfactoria; only in *Apteryx*, † *Dinornis* and *Dromaeus* there is a kind of lamina cribrosa with many openings (OWEN, 1866 II, pp. 130, 132; MARINELLI, 1936, p. 821). The plane of the fenestrae olfactoriae in the Sauropsida is more or less vertically situated (STADTMÜLLER, 1936, p. 919). But in the tropidobasic skulls of the Sauropsida an eventual skeletal encasement of the tractus olfactorius is usually not considered to belong to the cerebral capsule, so that here the nasal capsule does not adjoin the cerebral capsule; it lies at some distance in front of the cerebral capsule, it is situated precerebrally. In *Apteryx* and † *Dinornis* the nasal capsules extend so far in the caudal direction, that the rostral wall of the cerebral capsule forms the backwall of the nasal capsules and not of the orbitae, this in contrast to other Aves (OWEN, 1866 II, p. 64). In *Apteryx* with its strongly reduced eyes the ethmoidal part of the skull, according to MARINELLI (1936, p. 821, see also p. 817), is placed directly under the front part of the cerebral capsule ("unmittelbar unter der Vorderhirnkapsel") (the meaning undoubtedly is that it reaches to under this part of the cerebral capsule).

In the Mammalia the nasal capsule adjoins the cerebral capsule, as a consequence of the secondary platybasity. The position of the nasal capsule with regard to the cerebral capsule is determined by the size and the position (incline) of the plane of the fenestrae olfactoriae. Through these fenestrae olfactoriae, which are situated in the lamina cribrosa of the ethmoid, the nervus olfactorius or the fila olfactoria leave the brain case to enter the nasal cavity.

The area of contact between nasal capsule and cerebral capsule in the Mammalia can be small, when only one foramen nervi olfactorii is found; this occurs in *Ornithorhynchus* and secondarily in *Tarsius* and many Catarrhina and in some respects also in certain Odontoceti (WEBER, 1927 I, p. 217; STADTMÜLLER, 1936, pp. 892, 919, 989, 990, 992). All other Mammalia are characterized by a lamina cribrosa with many openings for the fila olfactoria (STADTMÜLLER, 1936, pp. 892, 919). In principle this means a larger area of contact between nasal capsule and cerebral capsule.

In Mammalia it is essentially the position and especially the incline of the plane of the fenestrae olfactoriae – consequently of the lamina cribrosa – (for this plane or this lamina separates the nasal cavity from the cranial cavity for the brain) which determines the position of the nasal capsule with regard to the cerebral capsule. In the lower Mammalia with their little developed brain, the lamina cribrosa has an all but vertical position, inclining a little from rostro-dorsal to caudo-ventral, the nasal capsule has mainly a precerebral position; only the hindmost part of the nasal capsule extends under the cerebral capsule; this is still the case in *Tarsius* (at the same time the nasal capsule has partly a pre-orbital position) (WEBER, 1927 I, p. 217; MATTHES, 1934, p. 928; STADTMÜLLER, 1936, pp. 891, 919). In the higher Mammalia, such as *Elephas*, Suidae, Dasypodidae and Primates, the lamina cribrosa is tilted forward and downward to some extent, assuming a more horizontal position, and consequently the nasal capsule lies partly or sometimes even all but completely subcerebral (KINGSLEY, 1925, p. 219; WEBER, 1927 I, p. 217; MATTHES, 1934, p. 928; STADTMÜLLER, 1936, pp. 891/892, 919, 980, 984, 992). In the Primates, this all but completely subcerebral position is a consequence of the great development of the brain and the reduction of the olfactory organ and of the upper jaw (MATTHES, 1934, pp. 928, 938; STADTMÜLLER, 1936, p. 958). The incline of the plane of the fenestrae olfactoriae entails a position of the nasal cavity ventral from the front part of the brain case, in *Nycticebus* and Anthropoidea, in contrast to *Tarsius* (STADTMÜLLER, 1936, p. 892). In addition to the influence of the brain on the lamina cribrosa, the preponderance ("Hervortreten") of the nasal skeleton in the Hylobatidae is determined by the alteration in the topography of the vomer (STADTMÜLLER, 1936, p. 956). In *Didelphis* also the plane of the fenestrae olfactoriae is almost horizontal; in this case, however, the cause is not the great development of the brain, but the development of the nasal capsules (STADTMÜLLER, 1936, p. 892). Also in *Tachyglossus* it is the great development of the olfactory organ which makes the olfactory organ find room under the telencephalon (MATTHES, 1934, p. 928).

The position of the nasal capsule with regard to the cerebral capsule is also partly determined by the incline of the upper jaw in relation to the cerebral capsule. For the nasal capsule lies on the upper jaw and there is a coordination between their longitudinal axes. We shall see later, that the upper jaw has a certain position, varying in different groups, with regard to the cerebral capsule. We will content ourselves with stating the fact, that Stadtmüller (1936, pp. 854, 892), after discussing the nasal capsule, points out that in Mammalia near the border of facial skull and cerebral skull, a downward deflection ("Abknickung") is found in the basis of the skull; this deflection ("Abknickung") is found on somewhat varying places and further it may be more or less pronounced or absolutely lacking. In the Holocephali we also find a downward deflection in the basis of the skull, caused by the fact that the brain curve at the junction of trabeculae and parachordalia has not disappeared (possibly due to the very large eyes), so that the front part of the skull is directed forward and downward (Holmgren & Stensiö, 1936, pp. 335, 336).

The position of the nasal capsule with regard to the orbitae is rather various.

In the primary platybasic skull the nasal capsule has a preorbital position. This is very clear in the Elasmobranchii; the two are separated by the processus praeorbitalis. In *Rana* the nasal cavity extends in caudal and lateral direction into the region of the cranial cavity, so that the cavum nasale is separated from the orbitae by the caudal wall of the nasal capsule (the planum antorbitale or the pars plana) (Stadtmüller, 1936, p. 552).

Also in the tropidobasic skull the nasal capsule has a preorbital position; the orbita separates cerebral capsule and nasal capsule. In *Apteryx* and † *Dinornis*, however, the nasal capsules extend caudally between the orbitae and the rostral wall of the cerebral capsule in the medial plane of the skull does not form the back wall of the orbitae, this in contrast with other Aves (Owen, 1866 II, p. 64).

In the secondary platybasic Mammalia, and as a consequence of the caudal extension of the nasal cavity, the os ethmoidale with its lamina cribrosa penetrates between the two orbitae that lie to the right and left of it; the lamina cribrosa separates nasal capsule and cerebral capsule. Whether and to what degree the nasal capsule of the Mammalia is pre-orbital, is dependent on the incline of the plane of the fenestrae olfactoriae and on the rostral extension of the nasal capsule.

f. Homology and non-homology

When comparing the size and the position of the nasal capsules we must not forget that the cavities of the nasal capsules are not everywhere strictly homologous. In this connection we may point to the extension of the respiratory and the vestibulary part. Connected with these differences in development are also the differences in the ethmoidal elements (one or two paired ossifications in Teleostomi, *etc.*), in the turbinalia, in the septum nasi of the Amniota, in the cartilage of the external nose in some Mammalia, *etc.*

5. UPPER JAW, UPPER BILL, ROSTRUM AND SNOUT

a. Introduction

It is not possible to treat the components of the skull mentioned above, separately and therefore they will be treated together.

The horny bill of Aves is so firmly attached to the skeletal nucleus of the upper bill that it is seldom known what place the skeletal upper bill occupies in the entire bill, including the horny covering. So in discussing the Aves we shall be obliged to point out the upper bill with its horny covering. The bills without the horny covering I could examine, showed that the outer surface of the skeletal upper bill lies immediately against the inner surface of the horny bill and that the horny covering is at the utmost but a few mms thick; thus the skeletal upper bill shows the shape of the outer surface of the upper bill, its measures being a few mms shorter in all directions.

The relation between the upper jaw and rostrum and snout is much more intricate.

In Elasmobranchii the primary upper jaw (palatoquadratum) and the primary rostrum are different morphological formations that can be clearly distinguished and have nothing to do with each other; at any rate they do not form a morphological whole in the shape of a snout or suchlike (see my fig. 61). The reason of this is that the palatoquadratum is situated ventral of the primordial neurocranium, so much caudalward that the opening of the mouth is ventral. (It is an exception when, in Elasmobranchii, the palatoquadratum has been displaced very far in a rostral direction such as in *Chlamydoselachus*, see my fig. 62.)

The other extreme is found in Mammalia where the snout is only formed by the nasal capsule and the new upper jaw, so that when the elements of the new upper jaw are taken away only the bony covering of the nasal cavity is left (see my figs 48, 49, 71 and 111). So it might be thought that if nasal capsule and upper jaw are discussed separately, it is no longer necessary to discuss the snout of Mammalia. But this is not so for two reasons. The combination of nasal capsule and pre-orbital part of the new upper jaw form a separate architectonic whole. In the second

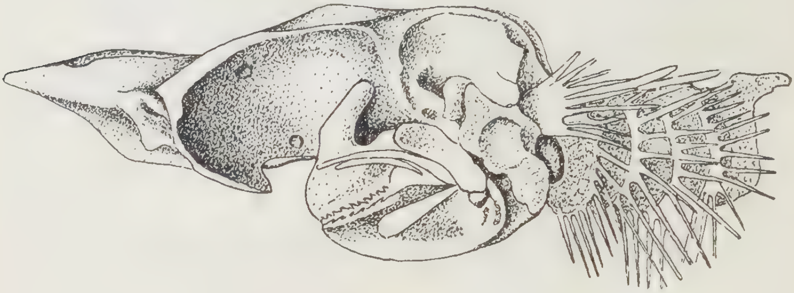

Fig. 61. *Squalus acanthias* L. Skull seen from the left side. After Marinelli, in Bolk, Göppert, Kallius and Lubosch (1936), IV, fig. 198 on p. 222.

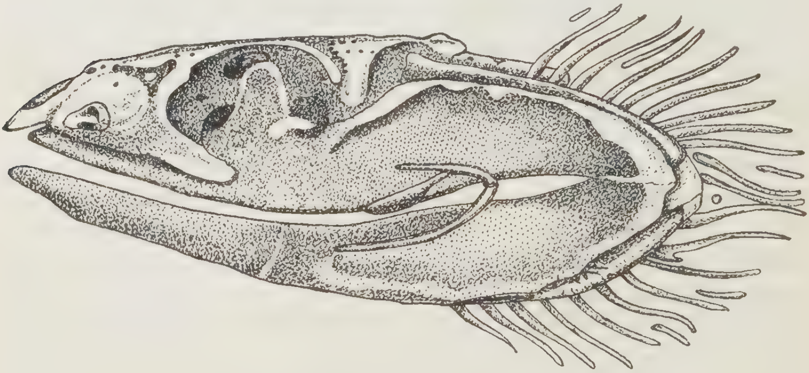

Fig. 62. *Chlamydoselachus anguineus* Garman. Skull seen from the left side. After Holmgren and Stensiö, in Bolk, Göppert, Kallius and Lubosch (1936), IV, fig. 240 on p. 307.

place the snout itself forms the pre-orbital part while, in Mammalia, the new upper jaw reaches farther caudally, below the orbita (see my figs 35, 37 and 58).

For the sake of completeness we may add that, in exceptional cases, things are not so simple in Mammalia. Thus a rostrum of the primordial neurocranium takes part in the formation of the snout in Cetacea, and in *Ornithorhynchus* a differentiated part of the nasal capsule forms the cartilaginous nucleus of the bill (STADTMÜLLER, 1936, pp. 893, 964).

In Vertebrata, which in the system are placed between Elasmobranchii and Mammalia, the relations between upper jaw, rostrum and snout are more intricate still.

In Pisces which are placed higher than Elasmobranchii, conditions diverge greatly and are very complicated. In my opinion we can distinguish three main types: in the first type we see conditions such as those we noticed in Elasmobranchii, that is to say, the rostrum forms a morphological whole that can be easily distinguished and separated from the upper jaw and they have no direct intimate connection (see my figs 61, 63); in the second type this intimate connection does exist, but the rostrum possesses a rostrally free part, protruding before the rostral point of the upper jaw (see my figs 76, 77); in the third type the rostral point of the upper jaw reaches as far as the most rostral part of the skull and the upper jaw is intimately connected with the rostrum, which, consequently, does not protrude any farther (see my fig. 86). In the second and third main types the rostrum and the upper jaw cannot be separately discussed. All the same it is not necessary for the discussion of the upper jaw to be absorbed by that of rostrum and snout. For, however rostrum and snout are defined they are in any case pre-orbitally situated components, whereas the back point of the upper jaw, the corner of the mouth, may be situated in very different places. If the corner of the mouth lies below the rostral ridge of the orbita, the discussion of upper jaw and snout might coincide in our third main type. But often the corner of the mouth lies much farther caudally, below or even behind the orbita (see my figs 87, 95) so that in our third main type the upper jaw is much longer than the snout. In some cases, however, the corner of the mouth lies before (see my figs 78, 79), sometimes even very much before the rostral edge of the orbita (see my figs 93, 117), and the upper jaw is situated at the end of a sometimes very long snout.

The phenomenon of the snout and the rostrum being more than the upper jaw plus the skeletal covering of the nasal cavity, is also met with in some of the higher Pisces. This phenomenon is especially clear in Teleostomi with a strongly developed secondary bony rostrum which serves as a bow or breakwater. This strong development of the secondary rostrum is certainly not due to the new upper jaw, for its pre-maxillary and maxillary elements are not very big and important (VERSLUYS, 1936, p. 717) and the function of the lining of the nasal grooves can easily be fulfilled by a small complex of bones. It follows that a number of other elements take part in the strong development of the secondary rostrum of Teleostomi. Thus in the lower Teleostomi we find a series of skeleton elements, such as the rostralia, interrostralia, postrostralia, basirostralia and antorbitalia, which, in different numbers, apart from each other or fused, either mutually or with other, surrounding elements, help to build up the secondary rostrum. Furthermore we find three nasalia in *Polypterus* and *Acipenser* and a number of lacrimalia in *Lepisosteus* (see my fig. 65) and *Lepidotus*, in the secondary rostrum (HOLMGREN & STENSIÖ, 1936, pp. 355, 365, 368 ff., 395, 442/443, 474, 475; STADTMÜLLER, 1936, p. 596).

In Teleostomi, too, we find here and there rests of the primary rostrum constituting the nucleus of and situated in the secondary rostrum. This is the case in † Belonorhynchidae, recent and fossil Chondrostei and Lepisosteidae, all groups with a very long secondary rostrum, in connection with which the opening of the mouth has a ventral situation in Chondrostei (HOLMGREN & STENSIÖ, 1936, pp. 422, 429, 469/470). In other Teleostomi the rests of the primary rostrum are very slight.

In Amphibia the new upper jaw reaches as far as the rostral point of the skull; this front point is generally rounded and the pre-orbital part of the skull is not very long so that, to our point of view, no special questions arise (see my figs 38, 39). In Amphibia the rests of the primary rostrum, the so-called processus praenasales inferiores medii do not protrude in front of the point of the snout (STADTMÜLLER, 1936, p. 562).

The phenomenon of the snout being more than the upper jaw plus the skeletal covering of the nasal cavity is also met with in Sauropsida. Thus I think I may conclude that in † Ichthyosauria and Aves the nasale does not only serve as a covering for the very small nasal cavity, but apart from that it has developed to help build up the snout and upper bill. From this it would be apparent that also in those cases where the outer opening of the nose is situated at the base of the snout or upper bill, this upper bill and snout are yet more than only the new upper jaw, also in the rostral part, so before the nasal capsule. For the rest we find a processus praenasalis as the nucleus of the upper bill in Aves.

So we cannot but come to the conclusion that upper bill, rostrum and snout cannot be discussed separately, but also that the upper jaw is often not absorbed by the snout, because the corner of the mouth is not necessarily situated on a level with the rostral edge of the orbita, but is, on the contrary very often situated more caudally.

Before indicating what, in this article, we mean by the terms upper jaw, primary and secondary rostrum and snout, it is necessary to consider the meaning of a number of terms used by GREGORY (1933) in this connection.

GREGORY (1933) uses the terms rostrum, snout, prolongation of the pre-orbital part of the face, trunk and proboscis, muzzle and ethmo-vomer block; he sometimes uses these terms indiscriminately and in his paper these terms are variously interrelated.

In Elasmobranchii GREGORY (1933, p. 101) speaks about a rostrum; so he uses this term for the primary, cartilaginous rostrum. By the side of this he also speaks of a bony rostrum with a variable composition produced in widely different families of Pisces (p. 440). So the secondary rostrum too is called rostrum by GREGORY. He does not emphatically mention where the backward limit of the primary rostrum lies. As the backmost limit of this does not necessarily lie on a level with the rostral edge of the orbita, but is generally situated a little more to the front, GREGORY's saying that the backmost limit of the rostrum does indeed lie there, is evidently applicable to the secondary rostrum. That GREGORY thinks that the back limit of the secondary rostrum lies on a level with the rostral edge of the orbita, may, I think, be concluded from his remark that the rostrum is connected with the interorbital bridge (p. 440), but especially from his definition of the effective rostral length as the distance from the prosthion (that is the most anterior point of the snout) or tip of the snout to the projection of the orbiton (that is the most anterior point of the orbita) upon the horizontal (that is the line joining the prosthion and the pygidion; pygidion being the mid-point of the narrowest part of the caudal peduncle) (p. 420). The question is now whether GREGORY calls, or might call, anything rostrum that has a pre-orbital situation, or whether he limits the use of the term to those cases wherein a part protrudes before the rostral edge of the upper jaw and (or) is slightly pointed. Indeed, the rostrum of *Rhynchoceratias*, which is called prominent, protrudes before the rostral edge of the upper jaw (p. 410) (see my fig. 63). The rostrum of *Istiophorus* is indeed a long narrow thin elongation of the skull which protrudes far rostrally beyond the rostral point of the lower jaw, but this rostrum is formed by elements of the new upper jaw itself (pp. 316/317). But GREGORY also speaks of a rostrum in Ostraciontidae, the skull of which is fundamentally identical with that of *Balistes*, where the ethmoid region shows a forward growth, leading to a great length of the pre-orbital face (p. 289, cf. pp. 286, 282/283, 290) (see my fig. 43).

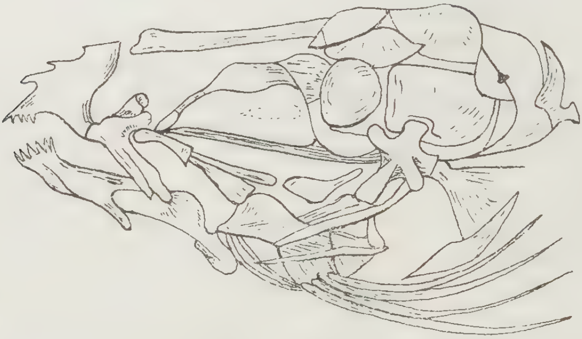

Fig. 63. *Rhynchoceratias*. Skull seen from the left side. After GREGORY (1933), fig. 281 on p. 409.

The term snout is very often used by GREGORY. Judging from the text of fig. 301 snout may, in GREGORY, be identified with the pre-orbital part of the skull, no matter whether this comprises the entire upper jaw, part of it, or more than the new upper jaw. GREGORY uses the term snout in many places where the skull has a blunt front while the opening of the mouth is terminal. Thus he gives as the difference between *Halosaurus* and *Notacanthus* that the former has a short, pointed rostrum, projecting beyond the mouth, and the latter genus has a very blunt snout (pp. 200, 201). But he ascribes a sharp snout to *Lates niloticus* (Gmel.) which, however, may refer to the transverse measurement and not to the longitudinal one (p. 242). For the rest he speaks about a round protruding snout in *Engraulis*, although this clearly reaches farther forward than the rostral point of the new upper jaw (p. 147) (see my fig. 76). In *Polynemus* he speaks of a growing snout and refers to a picture of *Polydactylus* (= *Polynemus*) where a knotty rostral excrescence makes the impression of a formation separating itself from the upper jaw, while the knob clearly reaches farther rostralwards than the rostral edge of the new upper jaw (p. 268). This state of things is much farther developed in Macruridae where the enlarged ethmoid forms a more or less projecting rostrum which protrudes separately from the rostral edge of the upper jaw (p. 382). So here Gregory again speaks about a rostrum, perhaps in order to give this separate protuberance a name of its own. Conversely he speaks about a snout in *Polyodon* although this is or contains a primary rostrum, which is completely separated from the farther caudally situated old upper and new upper jaw (p. 117). In a number of cases the terms rostrum and snout are used indiscriminately. Thus in *Acipenser* he speaks about a rostrum as well as a snout (p. 119) as he does also in *Esox masquinongy* Mitchill (p. 216) (see my fig. 30). In *Gonorhynchus gonorhynchus* (L.) Gregory speaks now about the pointed

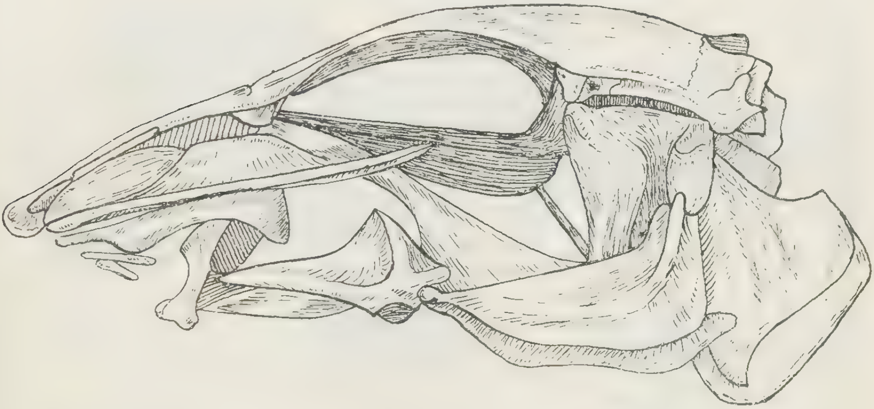

Fig. 64. *Gonorhynchus gonorhynchus* (L.). Skull seen from the left side. After Gregory (1933), fig. 66 on p. 177.

snout, now about the rostrum, of which he says that it is a blunt, projecting, bony rostrum (pp. 175, 176, 177) (see my fig. 64). The use of the term rostrum fits the fact of *Gonorhynchus* having a ventrally situated mouth and the new upper jaw not reaching as far rostralward as the rostrum. Above we saw already that, in the definition of the rostral length, GREGORY speaks about the prosthion as the most anterior point of the snout. So here, too, the terms rostrum and snout are used indiscriminately. In other cases snout means the same as strongly elongated jaws. In *Lepisosteus* GREGORY speaks about the great elongation of the snout, refering to the strongly elongated upper jaw, which ends at the terminally situated mouth (p. 127) (see my fig. 65). This is combined with the occurrence of accessory elements and elongation of other elements. Also in *Sphyraena* the elongation of the upper jaw is accompanied by a lengthening of the lacrimal and ethmoid region (p. 267). In yet other cases he calls snout what in other places he calls prolongation of the pre-orbital part of the face. This is the case in *Centriscus*, which shows a marked elongation of the snout, and which is compared to *Gasterosteus spinachia* L., where the pre-orbital face has already reached a further stage in the elongation of the pre-orbital part of the face (p. 226, see also pp. 224, 225). In *Rhamphichthys rostratus* (L.) the snout, which is very long, is compared to the form of the snout in certain Mormyridae, which show a tube-like prolongation of the pre-orbital part of the face (p. 189; see also p. 417). In *Gomphosus* he also speaks about a face elongated antero-posteriorly into a tubiform snout (p. 257).

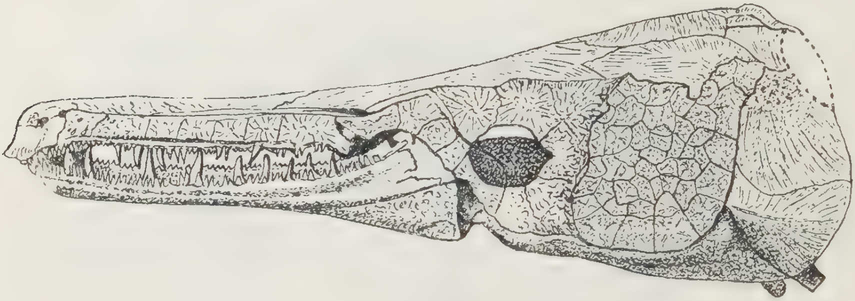

Fig. 65. *Lepisosteus platysomus* Rafinesque. Skull seen from the left side. After HOLMGREN and STENSIÖ, in BOLK, GÖPPERT, KALLIUS and LUBOSCH (1936), IV, fig. 363 on p. 475. Rostrale, antorbitale and nasale removed.

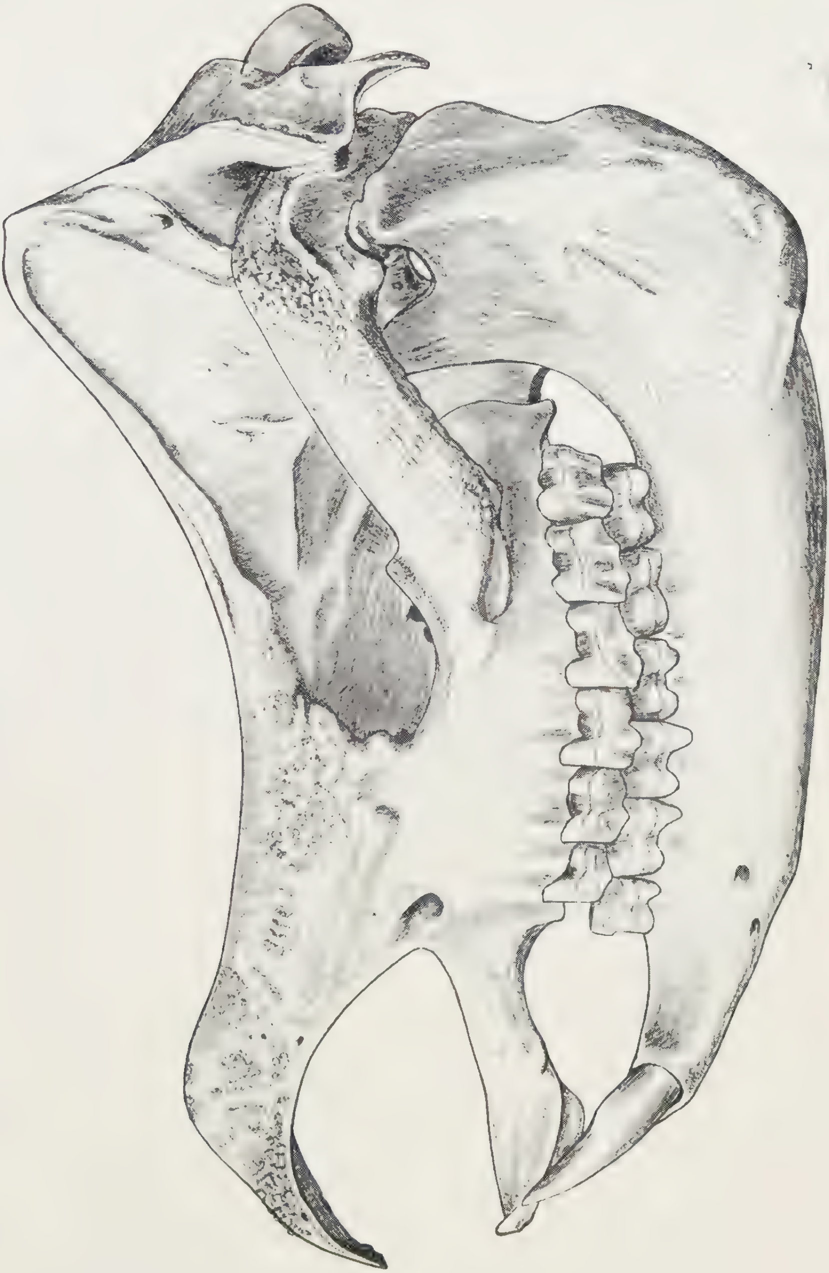

Fig. 58. *Rhinoceros sondaicus* Desm. Skull seen from the left side. 0.28×. Original drawing by Mrs M. IDENBURG in the collection of dr K. W. DAMMERMAN.

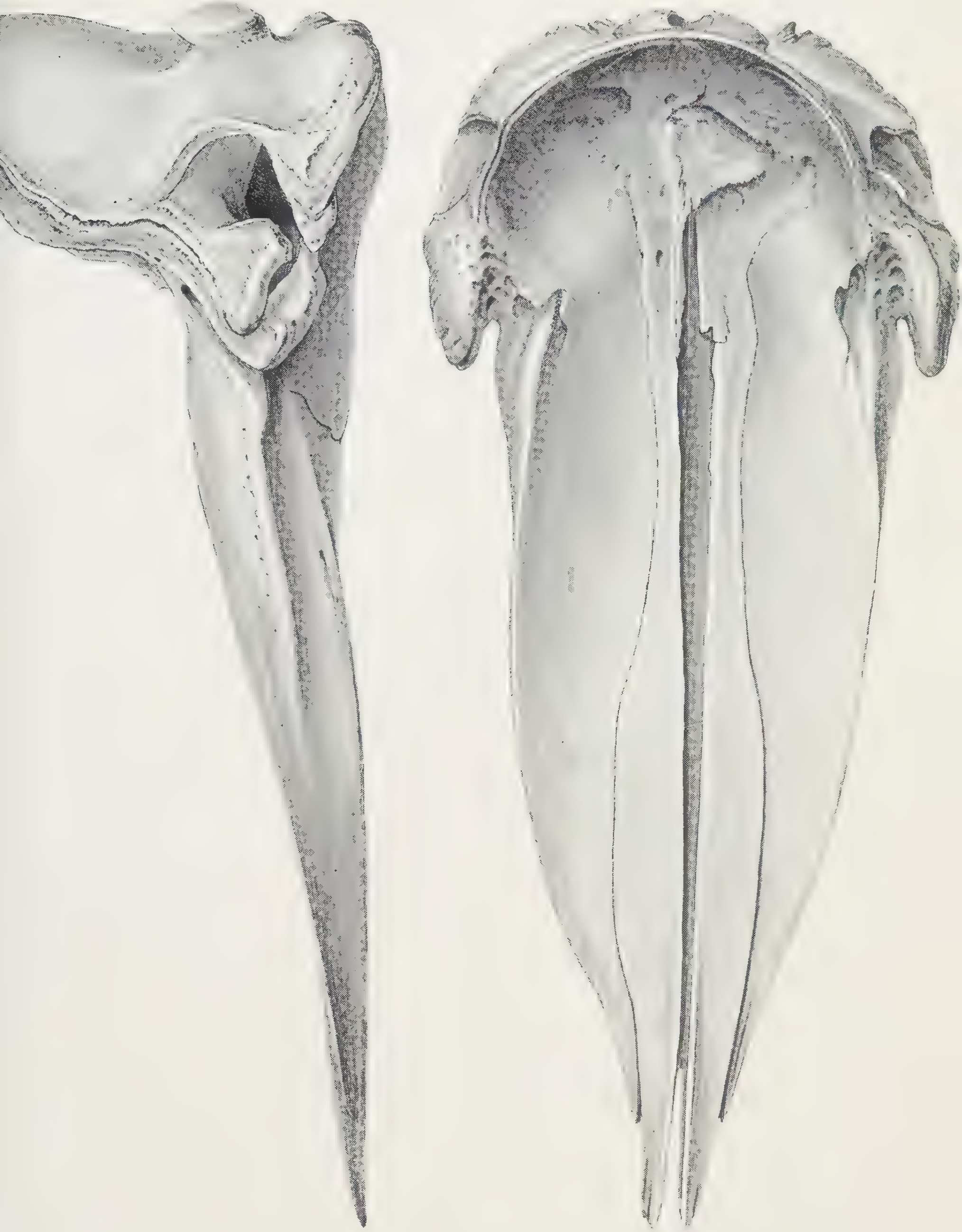

Fig. 59. *a. Physeter*. Skull seen from the left side. 0.03 . Original drawing by M. A. Koekkoek. *b. Physeter*. Skull seen from above. 0.03×. Original drawing by M. A. Koekkoek.

SIZE AND POSITION OF THE FUNCTIONAL COMPONENTS OF THE SKULL.

A CONTRIBUTION TO THE KNOWLEDGE OF THE ARCHITECTURE OF THE SKULL, BASED ON DATA IN THE LITERATURE

(Continuation)

BY

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Also the term elongation or prolongation of the preorbital part of the face, GREGORY uses in a number of places in a number of cases, *viz.* where the jaws are situated at the end of a strong elongation of the preorbital part of the skull, as is the case in Mormyridae (p. 417), in Thoracostei, such as *Gasterosteus*, *Aulostomus* and *Fistularia* (pp. 224, 225, 417; text of fig. 294) (see my fig. 93) and in Chaetodontoidei (p. 282) and in Balistoidei, among which are *Teuthis*, *Triacanthus*, *Balistes* (see my fig. 43), *Alutera* (see my fig. 91) and *Anacanthus* (p. 290, figs 165, 290). This prolongation is sometimes called tube-like (p. 417), sometimes it is excessive (text of fig. 294). This elongation is brought about in Chaetodontoidei by a prolongation of the lacrimal, the lateral ethmoid and the mesethmoid (p. 282). Above we already saw that GREGORY sometimes calls this prolongation snout.

So in Mormyridae GREGORY speaks about a tube-like prolongation of the preorbital part of the face, in other places he calls this a trunk, a "proboscis" (pp. 171, 172). In *Gnathonemus curvirostris* Blgr the trunk is long and decurved and has originated by the pulling out of the ethmoid, pterygoid and, if we include the lower jaw, of the articular bones (p. 171) (see my fig. 66). The corner of the mouth is *viz.* situated rather far backward, at a short distance before the orbita.

The term muzzle is used by GREGORY as well. In *Lagocephalus* and in Diodontidae he speaks of a shortening of the muzzle which is secondary with regard to the Balistidae, where this part of the skull is called preorbital part of the face (pp. 292, 293). The terms muzzle and snout are used indiscriminately as well (p. 445). Muzzle evidently does not indicate anything else than the other terms do. This is also apparent from the fact that GREGORY mentions of the muzzle of *Zoarces* that it is formed by the praefrontalia (parethmoidea) and the mesethmoid (p. 375).

Finally GREGORY uses the terms ethmo-vomer block and ethmovomerine block (p. 438). By these the main parts of the skull components mentioned above, are meant. In *Acipenser sturio* L. the main part of the ethmo-vomer block is the primary rostrum (p. 438) (see my fig. 74). In *Fistularia* (see my fig. 93) and in the Balistidae the ethmo-vomer block is the main part of the prolongation of the preorbital part of the face (p. 438).

So I think we may conclude that GREGORY (1933) does not make a sharp distinction between the ideas rostrum, snout, preorbital part of the face, muzzle and the like. But he does keep

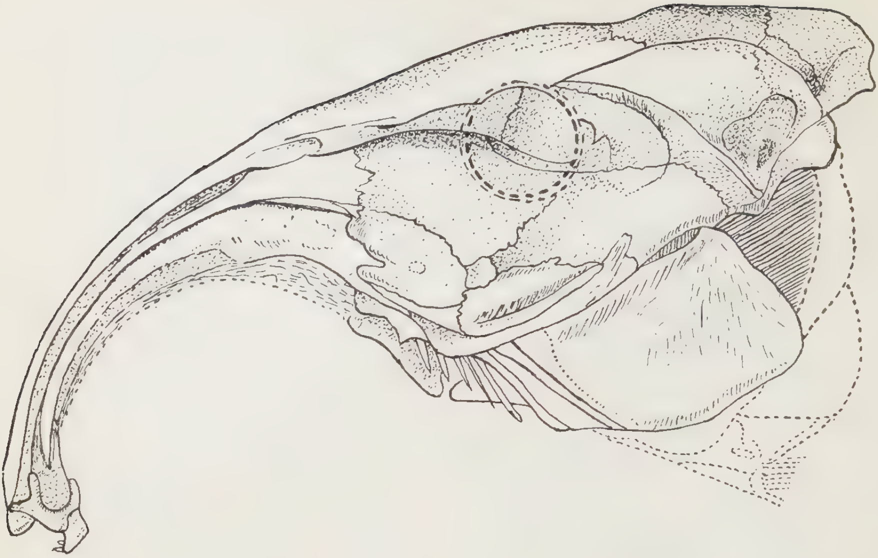

Fig. 66. *Gnathonemus curvirostris* Blgr. Skull seen from the left side. After Gregory (1933), fig. 63 on p. 171.

the term pseudorostrum for a separate formation which occurs in *Ogcocephalus vespertilio* (L.) (pp. 398, 399) (see my figs 23, 67 and 68).

In this article we shall group our records round the terms upper jaw, upper bill, rostrum and snout.

By upper jaw we shall understand the old upper jaw, the palatoquadratum of the Elasmobranchii, and the arcus palatoquadratus with its accompanying allostoses of the higher Vertebrata, as well as the new upper jaw, *i.e.* the praemaxillare and the maxillare. In the Vertebrata which are classed higher than the Elasmobranchii we shall only discuss the new upper jaw, unless a discussion of the old upper jaw by the side of it cannot be avoided. The old upper jaw of these higher Vertebrata will be discussed with the palate. So if we expressly limit the discussion of the new upper jaw to that of the praemaxillare and the maxillare, this purports that the region situated behind it, as far as the joint of the jaw, in other words the region of the arcus zygomaticus, will not be discussed in this paragraph.

By snout we shall understand the region before the front edge of the orbita, if this region partly or entirely contains the new

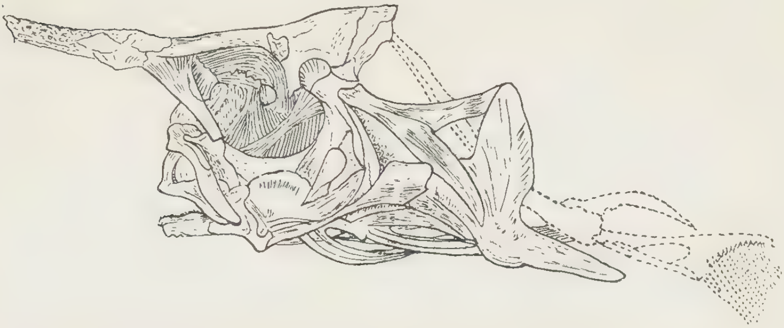

Fig. 67. *Ogcocephalus vespertilio* (L.). Skull seen from the left side. After Gregory (1933), fig. 269 on p. 397.

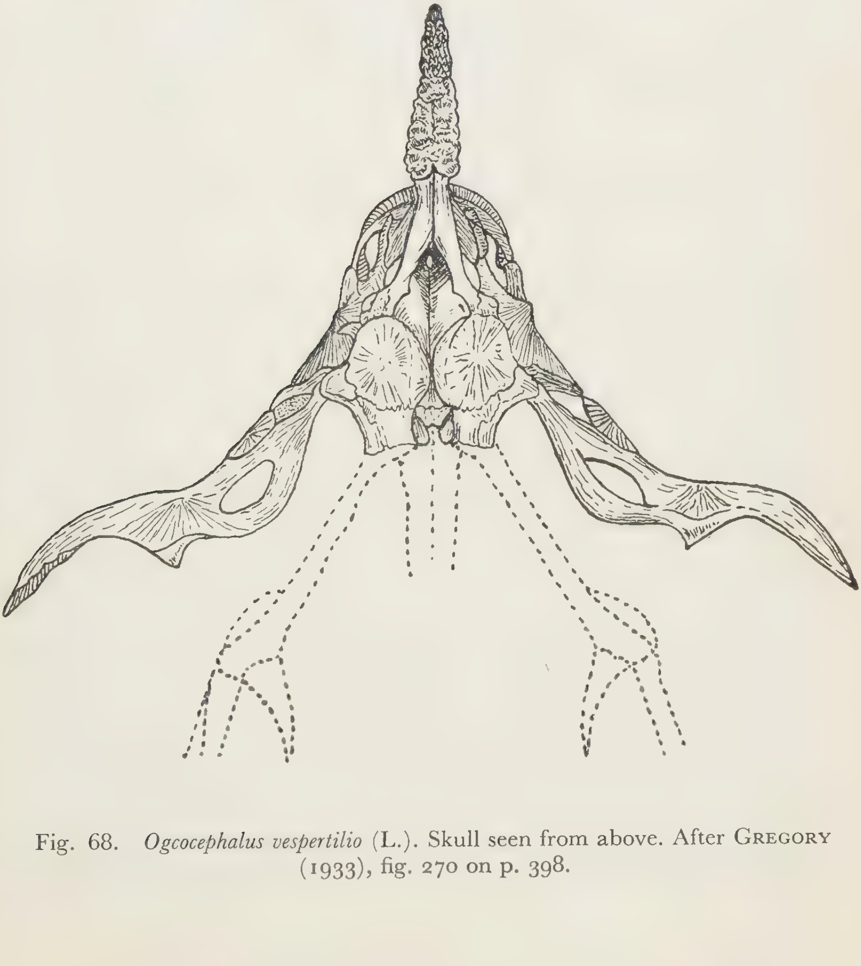

Fig. 68. *Ogcocephalus vespertilio* (L.). Skull seen from above. After Gregory (1933), fig. 270 on p. 398.

upper jaw. If this is not the case we have to deal with a rostrum. Apart from the new upper jaw – in part or complete – the snout also contains other parts such as the nasal capsule and accessory elements or fortifications and elongations of skeleton elements which help to build up the snout.

By rostrum we understand the primary as well as the secondary rostrum.

The primary rostrum is a cartilaginous, or cartilaginously preformated projection in the ethmoidal region before the front edge of the orbita, which projection remains separated from the upper jaw. For the rest anything that can be traced back to this projection, is called primary rostrum.

By a secondary rostrum we understand a projection of the skull in the preorbital region, consisting of allostoses, which protrudes farther in a rostral direction than the front edge of the new upper jaw, or which forms a separate projection over the front edge of the new upper jaw. So we only speak of a secondary rostrum when the slit of the mouth has a ventral situation. Consequently, in a much elongated, narrow upper jaw with a terminal mouth opening, we shall not speak of a rostrum, but of a snout.

b. The size and shape of upper jaw, upper bill, rostrum and snout

In the literature I worked through I did not find exact data about the size of upper jaw, upper bill, rostrum and snout. As a rule data about the size only refer to length in a longitudinal direction. To obtain an insight in the size, shape, and, consequently, other measurements, must be taken into account as well.

The absolute size and shape of upper jaw, upper bill, rostrum and snout

Direct data about the absolute size of these components of the skull seldom occur. Data which give no further information on the nature of the reports on size, will nearly always refer to relative size.

Generally speaking, the primary rostrum and palatoquadratum of Elasmobranchii are absolutely large in the large species and absolutely small in the absolutely small species. There are, however, some Hypotremata where the primary rostrum is almost entirely lacking (HOLMGREN & STENSIÖ, 1936, p. 309).

In Teleostomi as well, the absolute size of upper jaw and snout depend on the absolute body size of the species. A considerable absolute size is rare, because species with a very large absolute body length seldom occur. Sometimes the absolute length of the new upper jaw is relatively large, whereas the absolute size of the snout is small; this is the case when the eye has a marked rostralward situation while the corner of the mouth is situated far caudalwards behind the eye. We shall treat these cases below with the discussion of relative size.

But for some exceptions among the Caudata *e.g.*, recent Amphibia reach a small absolute body size, so that the absolute size of the new upper jaw is small, too; the absolute size of the snout is small, generally very small.

Among † Stegocephala there are species with a considerable absolute body size; in this case the absolute size of the new upper jaw is considerable, and at the same time the absolute size of the snout is large. In † Stegocephala the elements of the new upper jaw are more important and larger than in Teleostomi (VERSLUYS, 1936, p. 717).

Also among the Reptilia there is a certain connection between the absolute size of the new upper jaw and the snout on the one hand and the absolute size of the body on the other in this sense that absolutely small animals also have absolutely small upper jaws and snouts, and the reverse. On the one hand we point to the small Sauria, Serpentes, Testudinides, *etc.*, on the other hand to all kinds of very large species among Loricata, Sauria, Serpentes, Testudinides; also among † Phytosauria, † Ichthyosauria and other marine groups.

In Aves, too, there is a connection between the length of the upper bill and the absolute size of the body. According to MARINELLI (1936, p. 811) the length of the bill generally conforms more closely to the size of the body, than the brain does. When discussing the relative size of the upper bill we shall see that there are many exceptions to this. Absolutely large upper bills are found in many absolutely large Birds among the stilt-birds, the Rhamphastidae (see my fig. 69), the Bucerotidae *etc.* Even in the biggest Aves the absolute size of the upper bill is never exceptionally large because the size of the body is always limited as well. Absolutely small upper bills are found in absolutely small Birds.

Among Mammalia the upper jaw is absolutely very large in absolutely very large animals such as big Cetacea, *Elephas*, "*Rhinoceros*", *Hippopotamus etc.* The upper jaw is absolutely small in absolutely small Mammalia such as many Insectivora, Rodentia *etc.*

In determining the absolute size of the upper jaw and the snout, we must not only pay attention to the length in a longitudinal direction, but also to the measurements in the two other directions. Thus the upper jaw, upper bill and snout may be very large in a longitudinal direction, but breadth and height may be very small, so that the volume is, after all, not very great. In this connection we are reminded of upper jaw and snout of long-snouted Gavialidae (see my fig. 100), of very many Aves, and of the Cetacea. The slight height of the upper bills of such Aves and of the upper jaw of Cetacea entails that the transition from the curve of the brain skull into the upper bill in such Birds, and into the upper jaw in Cetacea, may be very abrupt and far from gradual (see my figs 14, 36, 70 *b* and 98).

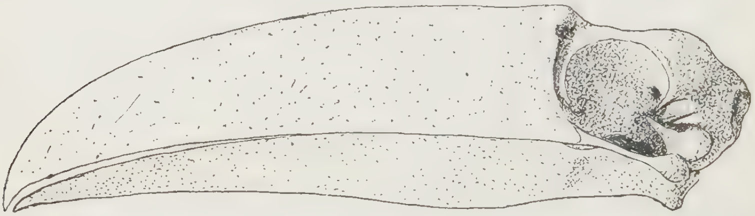

Fig. 69. *Ramphastos monilis* Müller. Skull seen from the left side. R.M.N.H. Leiden, no. 6837. 0.6×. Original drawing by J. F. Obbes.

The absolute size of the new upper jaw and the snout does not only depend from the absolute size of the body, but also from other factors. Indeed, big animals need a large quantity of food, and, connected with this, the upper jaw is often relatively big in proportion to that of smaller species of animals, so that, in absolutely big animals the upper jaw is absolutely big. But the size of the new upper jaw depends more directly on the development of the teeth, the chewing-muscles and the chewing-mechanism (Stadtmüller, 1936, p. 956). Now, these three last-mentioned factors depend on a great number of other factors among which we include the size of the animal, but they also depend, in the first place on the use of the upper jaw in feeding, and in the second place on the use of the jaw in the mastering and the consumption of the food (in the last two cases they consequently depend on the character of the food as well) and in the third place on some additional factors that play a part in the development of the size of the new upper jaw, such as the function of the teeth as a weapon, of the teeth and the upper bill in sexual play, the function of the jaws as a seizing-organ *etc.* (WEBER, 1927 I, pp. 234/235). That is why the absolute size of upper jaw and snout may be very different in animals of equal size. We shall discuss these phenomena exhaustively at the hand of examples, when discussing the relative size of upper jaw, upper bill and snout.

The relative size and shape of upper jaw, upper bill, rostrum and snout

Exact data on the relative size of these components of the skull are lacking or extremely rare. Even in the statements in literature it is not always clear whether the relative size is meant with relation to the size of the head, or that of the body.

In stages of development

Among Teleostei it is usual in the late embryos, larvae and fry that the mouth and the jaws, thus also the new upper jaw, are at first very small and the snout extremely short; this arrangement in earlier developmental stages may in many forms tend to be retained in the adult; as ontogenetic development proceeds, in many Teleostei the snout begins to lengthen as well as the jaws, so that the predaceous jaws become more prominent (GREGORY, 1933, pp. 327, 422/423, 428/430, 431, 443, 445).

If and in so far as the crossing of the points of the bill in the adult *Loxia curvirostra* L. should entail a difference in the relative length of the new upper jaw itself with regard to the youth stages, the fact should be mentioned that in the nestling the bills are still symmetrical, in other words, the upper bill is straight (BÖKER, 1937, p. 26).

In those Aves where the upper bill shows an exceptional length or curve in the adult animal, this is not the case in its youth (BÖKER, 1937, pp. 63/64); in how far this influences the relative length of the skeletal upper jaw, I do not yet know¹).

In adult animals

Data on the relative size of upper jaw, upper bill, rostrum and

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¹) For the increase of the relative length of the preorbital part in Mammalia, see: R. CUMMING ROBB (1935), J. Genetics **31**, pp. 47—52. (Postwar addition in the manuscript)

snout, in literature, refer to this size with regard to the cerebral capsule and cerebral skull, with regard to the length of the neck and finally with regard to the size of the entire skull or the entire head or the entire body.

The relative size of upper jaw and snout with regard to the cerebral capsule and the cerebral skull, is mentioned in literature with regard to related races, and in homoneuric species.

In domesticated *Oryctolagus cuniculus* (L.) the relation between facial and cerebral skull, as compared to wild *Oryctolagus cuniculus* (L.), has changed; in this change the length of upper jaw and snout is involved, for they form the main part of the facial skull (Böker, 1937, p. 193).

In homoneuric species of animals the smaller species have, relatively, the bigger cerebral capsule; in other words a relatively short upper jaw, and the reverse (see my figs 6 and 8). Dubois (1898, pp. 437, 438) draws attention to the fact, that the median projection of the dentition in an old *Panthera tigris* (L.) has about three times the length of that of *Felis catus* L., the length of the cerebral skull being only about twice as long. If the enlargement of the surface of the brain in the larger tiger in comparison to the cat had taken place in the same way as in *Homo*, the length of the brain would have been only 1.38 times that of the cat. In that case an attachment of the long jaw would have been difficult. Due to this the enlargement of the surface of the brain in those Mammalia which show a well developed dentition, is attained by enlargement of the volume of the brain, according to Dubois. In *Homo*, however, there is no objection to the enlargement of the surface of the brain by folding of the surface, as the jaw is relatively very short, whereas the smaller size of the brain thus achieved is an advantage.

The relative size of the upper jaw and snout with regard to the length of the neck is mentioned in literature here and there too.

In † Plesiosauria, according to Williston (1925, p. 56): "The general shape of the skull seems to bear a definite relation to the length of the neck, always shorter in the long-necked forms, slender, sometimes very slender in the short-necked types". This may be applied to the relative size of upper jaw and snout with regard to the length of the neck, because the general shape of the skull and especially the fact whether the skull is more or less slender is closely bound up with the relative length of snout and upper jaw with regard to the cerebral skull.

In Mammalia the connection between the length of the neck and that of the new upper jaw and snout, is not so simple. There we find very heavy heads and skulls combined with short necks (*Elephas*, *Hippopotamus*, "*Rhinoceros*", *Sus*), whereas a light head and skull may be found in combination with a very long neck (*Giraffa*). The length of upper jaw and snout in Mammalia, however, does not only depend on the general relation of the relative size of the cerebral skull to the size of the new upper jaw and snout, – decided by the size of the entire head – but also on the relation between the length of the neck and that of the forelegs. For, with a short neck, upper jaw and snout may be very long if the forelegs are short (*Hippopotamus*, "*Rhinoceros*", *Sus*) (see my figs 49 and 71), but the bony upper jaw and snout may be very short when the forelegs are long, provided that a trunk has developed (*Elephas*) (STADTMÜLLER, 1936, p. 952).

The relative size of the upper jaw, upper bill, rostrum and snout with regard to the size of the whole skull or the rest of the skull, with regard to the size of the head and also with regard to the size of the body, must be treated together, because, in literature, it is not always clear whether the indication of the relative size of upper jaw or snout *etc.* refers to the relation with regard to the size of the skull, or to the size of the rest of the skull, or to that of the head, or even to that of the whole body.

Before giving the data from literature in this respect, we must touch upon two points: the difference between the longitudinal measurement in one direction and the volume of the upper jaw *etc.*, and then what factors influence the relative size of the upper jaw *etc.*

When mentioning the size of the upper jaw *etc.*, we should ask ourselves whether this indication refers to the linear measure in a longitudinal direction, or to the volume, wherein, consequently, the measurements in the two other directions have been assimilated. A relatively very long snout may have very little breadth and height, so that such a snout need, also relatively, not be larger as regards volume, than a short but broad and high snout.

The relative size of upper jaw, upper bill, rostrum and snout is influenced by a number of factors. Whenever we know of an explanation of the relative size on account of one of these factors, or when such an explanation is possible or probable, we shall point this out in the following, when mentioning the data. But first we shall mention these factors.

The relative size of the upper jaw depends on the size of the body, but also on other factors. Above we saw that, in related races and homoneuric species of animals, the upper jaw is often relatively small compared to the cerebral skull in small races and species, and relatively large in comparison to the cerebral skull in large races and species. Furthermore, large animals need a great quantity of food, and, connected with this the upper jaw is relatively large compared to that of the small species of animals. So there is no proportion between the size of the upper jaw on the one hand and the size of the cerebral skull, the entire skull, the head or the entire body on the other hand, even in closely related species. MARINELLI (1936, p. 811) it is true, mentions, as we saw above, that in Aves the length of the bill generally conforms more to the size of the body than the size of the brain does. But to this there are such a number of exceptions that it is hardly possible to speak about a connection between the length of the bill and the size of the body, because the bills of all Birds, even those of related Birds do not serve one special function *e.g.* the seizing of food; and also when they do serve an identical purpose the sort of food is not identical and the place or the environment where the food is seized is not identical either. The dependence of the size of the upper jaw, upper bill *etc.* on the size of the head and the body, is crossed by many other dependences.

In discussing the absolute size of the upper jaw we saw that the size of the new upper jaw is more directly dependent on the development of the teeth, of the chewing-muscles and the chewing-mechanism (STADTMÜLLER, 1936, p. 956). These three factors are indeed partly connected with the size of the body but they are also connected with, in the first place, the use of upper jaw and upper bill in taking and holding the food, in the second place, the use of the upper jaw *etc.* in mastering and cutting up the food (in the two latter cases it depends, consequently, on the sort of food) and in the third place with some additional factors (WEBER, 1927 I, pp. 234/235). As examples of the third series we mention the use of the teeth as a weapon, which influences the relative size of the upper jaw (*Elephas*, Carnivora), the part the teeth of Mammalia and the upper bill of Aves play in the sexual play (Bucerotidae, Rhamphastidae) (see my figs 15 and 69), the use of teeth and bill as a grasping organ (grasping of nesting material, gripping of branches for locomotion in climbing), the use of the teeth in digging (biting through roots of plants) *etc.* Therefore the relative size of upper jaw and upper bill may differ greatly in animals that are closely related but differ in size of body, or in animals of identical size of body but different way of living.

The relative size of the snout with regard to the size of the rest of the skull, of the entire skull, of the head or of the entire body is not directly connected with the relative size of the upper jaw and upper bill, because the size of the snout is determined by the situation of the orbita, and the orbita has no fixed situation with regard to the corner of the mouth or the front point of the upper jaw or upper bill. With a frontal situation of the eyes, such as in *Homo* and in *Rupicapra rupicapra* (L.), the snout is relatively very short. The proportion between length, breadth and height of the snout is much influenced by a digging or grubbing way of living, in such a case the head is wedge-shaped, and the shape of upper jaw and snout greatly contribute to this wedge-shape (see my fig. 49).

The relative size of the rostrum is, among other things, connected with the function of the rostrum as an organ for grubbing up food from the ground, with the function of weapon, and as an elevation rudder for the diving body.

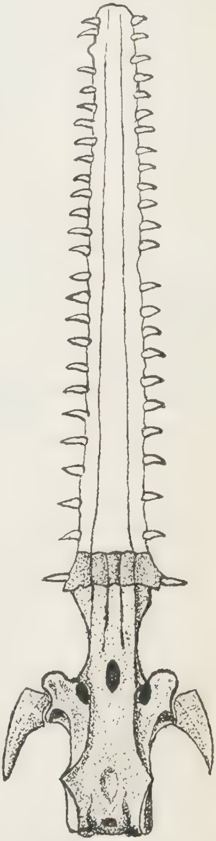

Fig. 72. *Pristis pectinatus* Latham. Skull with rostrum seen from above. 0.24×. After L. Hoffmann (1912), fig. 22 on plate 16 and fig. 14 on plate 14 (combined).

Among Pisces most Elasmobranchii have a well developed primary rostrum (see my fig. 61). In Selachii the primary rostrum is relatively well developed in a longitudinal direction. In Hypotremata the primary rostrum is generally relatively long, sometimes very long, whereas the primary rostrum in those Hypotremata where it is almost entirely lacking, is extremely small (Holmgren & Stensiö, 1936, p. 309). In Pristidae it is relatively very long (Böker, 1937, p. 24) (see my fig. 72). As regards the measurements in Elasmobranchii in the other directions, GREGORY (1933, p. 101) mentions that the primary rostrum is more or less broad and depressed and that this depression and widening is pronounced even in *Mustelus*. It becomes excessive in *Sphyrna tiburo* (L.) (*Zygaena*), where an extreme transverse growth of the front end of the head occurs in the form of suddenly projecting shelves (GREGORY, 1933, pp. 101, 102) (see my fig. 73). Probably this indication of the relative size in GREGORY, as everywhere else, refers to the size with regard to the rest of the skull or to the entire skull.

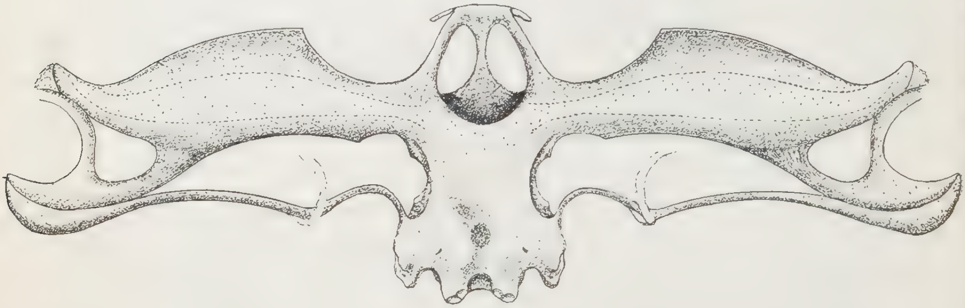

Fig. 73. *Sphyrna* Rafinesque (*Zygaena* Cuvier). Skull seen from above. Reduced size. After C. GEGENBAUR (1872), Taf. IX, fig. 1. Right side of the skull added. Dotted line indicates the extension of the nasal groove.

A few data about the relative size of the primary rostrum and the secondary rostrum of the higher Pisces may follow here[1]).

In *Polyodon* the primary rostrum, what GREGORY calls the snout (1933, p. 117) shows a great development.

In literature we find more data on the relative size of a secondary rostrum in the meaning which we attach to it, *viz.* a projection of the skull in the preorbital region, consisting of allostoses, which projection protrudes farther rostrally than the front edge of the new upper jaw, or forms a separate projection over the front edge of the new upper jaw. In *Acipenser* the secondary rostrum, called snout by GREGORY (1933, p. 119) is well developed (see

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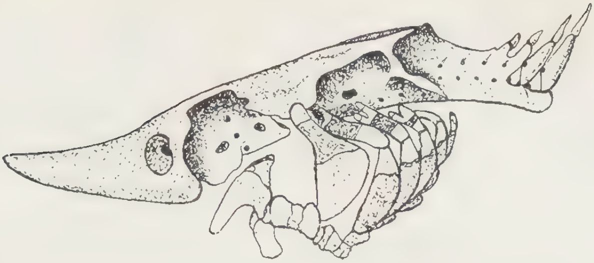
[1]) On the snout of Crossopterygii and lower Gnathostomata in general, see: E. JARVIK (1942), Zoologiska Bidrag fran Uppsala **21**, pp. 235—675; on the jaws of the earliest known fossils, see: W. K. GREGORY (1943), Amer. J. Orthodontics and oral Surgery **29**, pp. 253—276. (Postwar addition in the manuscript)



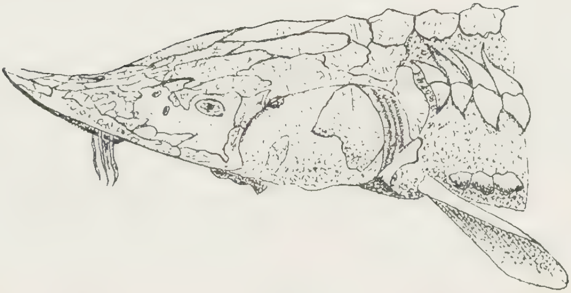


Fig. 74. *a. Acipenser* sp. Neurocranium with splanchnocranium, seen from the left side. After MARINELLI (1936), fig. 195 on p. 212.

Fig. 74. *b. Acipenser* sp. Dermatocranium and rostral part of the body, seen from the left side. After MARINELLI (1936), fig. 195 on p. 212.

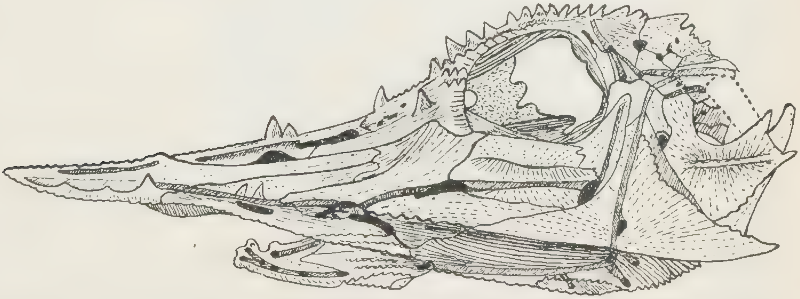


Fig. 75. *Peristedion cataphractum* (Gmel.). Skull seen from the left side. After GREGORY (1933), fig. 220 on p. 339.

my fig. 74). In *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*) there is a bony rostrum, which GREGORY calls pointed snout (GREGORY, 1933, pp. 175, 176, 177), which is elongated and blunt projecting (see my fig. 64). *Peristedion* as well has a sturgeon-like appearance of the head, which means that there is a secondary rostrum as we understand it, which is relatively very long (Gregory, 1933, p. 343) (see my fig. 75). The pointed, bony rostrum in *Halosaurus* is short (p. 200). In *Rhynchoceratias* the secondary rostrum is prominent, it protrudes rather far before the front point of the new upper jaw (p. 410) (see my fig. 63). In *Engraulis* the secondary rostrum, in the shape of a round protruding snout, as Gregory calls it (1933, p. 147) sticks out farther than the front point of the new upper jaw (see my fig. 76). In Macruridae as well there is a more or less projecting rostrum (p. 382). Gregory (1933) gives pictures of a secondary rostrum in *Albula*

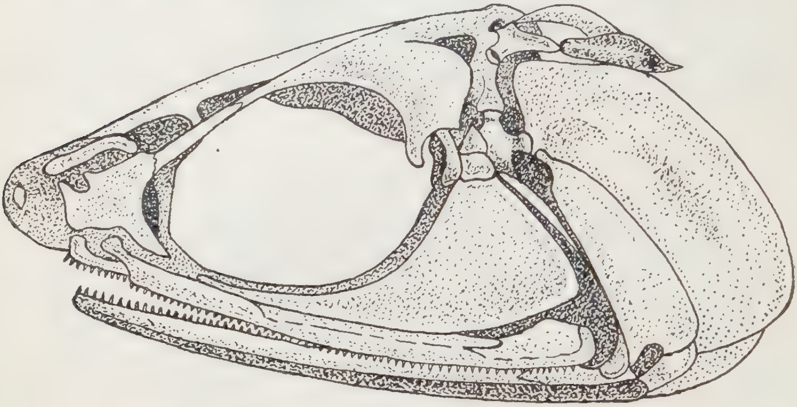


Fig. 76. *Engraulis encrasicholus* (L.). Skull seen from the left side. After Gregory (1933), fig. 40 on p. 148.

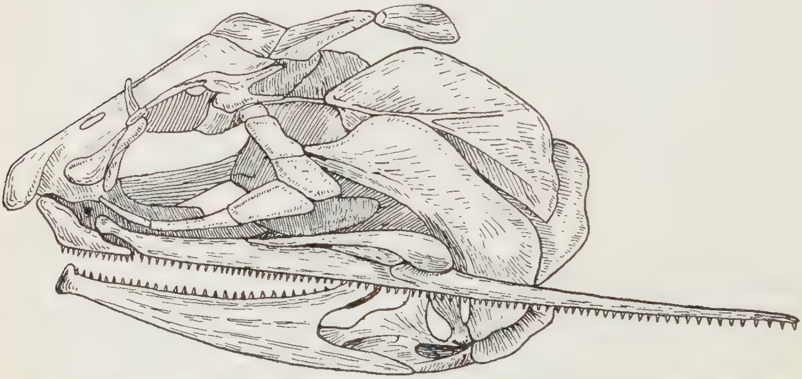


Fig. 77. *Coila nasus* Temm. Schl. Skull seen from the left side. After Gregory (1933), fig. 41 on p. 148.

vulpes (L.) (fig. 37) (see my fig. 125), *Coila nasus* Temm. Schl. (fig. 41) (see my fig. 77) and *Esox masquinongi* Mitchill (fig. 95) (see my fig. 30).

In *Ogcocephalus vespertilio* (L.) the pseudorostrum is relatively large (GREGORY, 1933, pp. 398, 399) (see my figs 23, 67 and 68).

In the discussion of the relative size of the upper jaw, we have, according to the idea of this paragraph to deal with the old upper jaw in the case of Elasmobranchii, and with the new upper jaw in the case of the higher Vertebrata.

Among Elasmobranchii, *Chlamydoselachus anguineus* Garman shows a long, slender almost snake-like jaw (see my fig. 62). At the other extreme of the true Selachii we have the massive, short jaw of *Heterodontus* (*Cestracion*). Between these extremes stand the moderate to small-sized jaws of the squaloid sharks (GREGORY, 1933, p. 102).

In Pisces, which are classed higher than the Elasmobranchii, we should, in accordance with the idea of this paragraph, have to discuss the relative size of the new upper jaw, and the region situated behind it, as far as the quadratum-articulare joint would not come into discussion. This idea, however, brings us into a number of difficulties in the case of the higher Pisces. There are indeed a number of cases where the new upper jaw reaches from its front point in the direction of the quadratum-articulare joint in the same way as in higher Vertebrata. But the cases where the Pisces show a different condition are numerous too. We may arrange these divergencies under the following headings: 1. Sometimes the maxillare reaches farther caudally than the quadratum-articulare joint. 2. In many cases the new upper jaw crosses the lower jaw rostral of the quadratum-articulare joint, in this way shortening the slit of the mouth, and sometimes forming a second corner of the mouth with a more rostral situation. 3. In a number of cases the new upper jaw, by its toothlessness and also by its shape, makes the impression that it has not the function of a jaw. In such diverging conditions the praemaxillare and maxillare evidently have another function than that of the jaw, namely the function to border the gape (GREGORY, 1933, pp. 186, 187, 193, 201).

In the diverging condition first mentioned, the maxillare reaches farther caudally than the quadratum-articulare joint. This is the case in *Coila nasus* Temm. & Schl. where the maxilla is produced backward far behind the skull into a long, narrow, denticulate rod (Gregory, 1933, p. 147, fig. 41) (see my fig. 77). Judging from more pictures in Gregory (1933) the maxilla clearly reaches farther caudalward than the quadratum-articulare joint in *Tarpon atlanticus* C. & V. (fig. 31) (see my fig. 85). This is evidently the case, to a slight degree, in *Microspathodon*

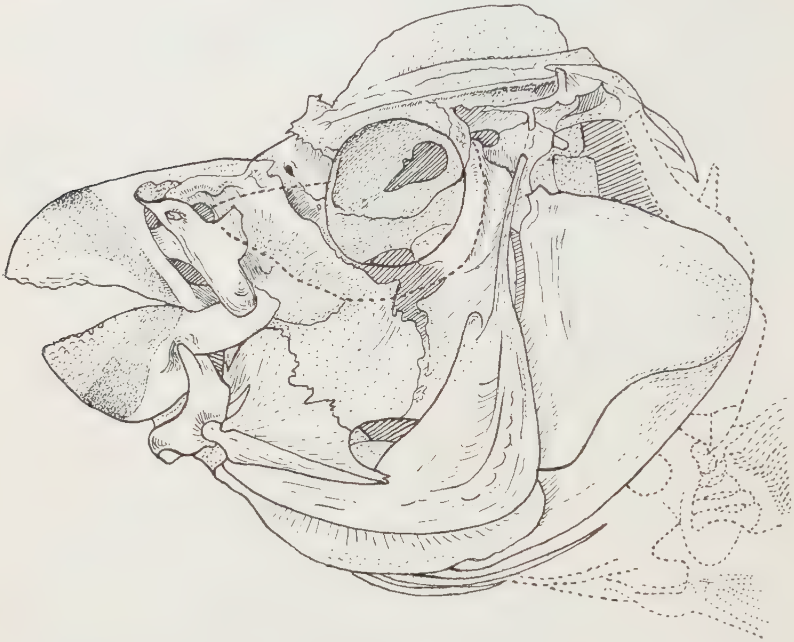


Fig. 78. *Pseudoscarus guacamaia* (Cuv.). Skull seen from the left side. After Gregory (1933), fig. 133 on p. 259.

chrysurus C. & V. (fig. 128) and in *Scorpaena plumieri* Bl. (fig. 201). Perhaps it also reaches a little farther backward in *Chirocentrus dorab* (Forsk.) (figs 34, 288 C), in *Hepatus triostegus* (L.) (fig. 156) and possibly also in † *Cheirolepis* (fig. 286 A, also 12 A) (see my fig. 95), † *Coccocephalus* (fig. 286 B, also 12 C), † *Perleidus* (fig. 286 C, also 21 A, 283 C) and † *Platysomus* (fig. 286 D, also 15 B) (see my fig. 90).

As a second diverging condition we saw the phenomenon that in many cases the new upper jaw crosses the lower jaw rostral of the quadratum-articulare joint, in which case the slit of the mouth is shortened and a second corner of the mouth is formed. This phenomenon may be connected with the fact that the praemaxillaria and maxillaria do not so much function as jaws, but are rather elements whose task it is to border the gape. In connection with this these elements are situated within the margin of the slit of the mouth.

GREGORY (1933) emphatically mentions that a second, more rostrally situated corner of the mouth occurs in certain genera of the Scaridae, genera where also the dentale forms a secondary joint with the articulare (see my fig. 78); in these genera the maxilla is attached below to the ascending process of the dentale, with the result that the gape of the mouth is reduced (pp. 257/258).

In *Cyprinus carpio* L. and allied Eventognathi the ascending process of the dentale is also situated against the maxilla (GREGORY, 1933, pp. 190/191). In the cyprinid *Aspius aspius* (L.) (*Aspius rapax*) the ascending process of the dentale lies further back, as the typical carp mouth has been modified toward predatory habits (p. 193). The phenomenon of the protrusility of the mouth which occurs in Ostariophysi and in Acanthopterygii is combined with an attachment of the lower end of the maxillare with the lower jaw, so that a downward movement or depression of the lower jaw pulls down the lower ends of the maxillaria mentioned above, *e.g.* by means of the ascending process of the dentale; the maxillare, in its turn, moves the praemaxillare (GREGORY, 1933, pp. 190/191, 242, 257, 424). A condition for protrusility is also a small gape; the enlargement of the jaws, as in *Sphyraena*, has reduced the protrusility of the praemaxillaria almost to zero (pp. 242, 267). The relativity of the idea "a small gape" is made evident by *Scorpaena scrofa* L., which is mentioned as an example of protrusility, and, consequently must have a small gape, whereas the picture shows a very long maxillare, and also the intersection of the lower edge of the maxillare and the lower jaw is situated far backward in this picture (GREGORY, 1933, p. 424, figs 116, 203) (see my fig. 79). Perhaps, however, the degree of protrusion influences this.

The idea "small gape", which is so little exact in itself, as we saw in what is written in connection with *Scorpaena scrofa* L., must be used with the utmost reserve, if we meet it in GREGORY. Therefore it does not indicate more than a possibility that GREGORY, in the cases that will be mentioned in the following, means the distance to the point where the new upper jaw and the lower jaw cross each other, when he uses the term "a small mouth" and

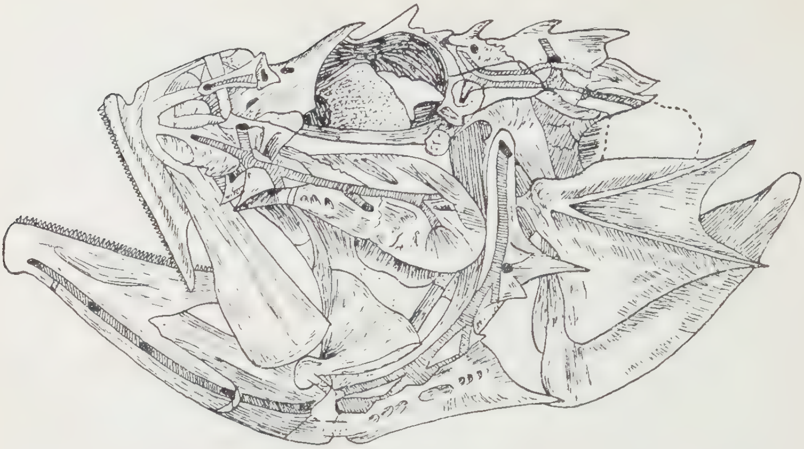


Fig. 79. *Scorpaena scrofa* L. Skull seen from the left side. After Gregory (1933), fig. 203 on p. 324.

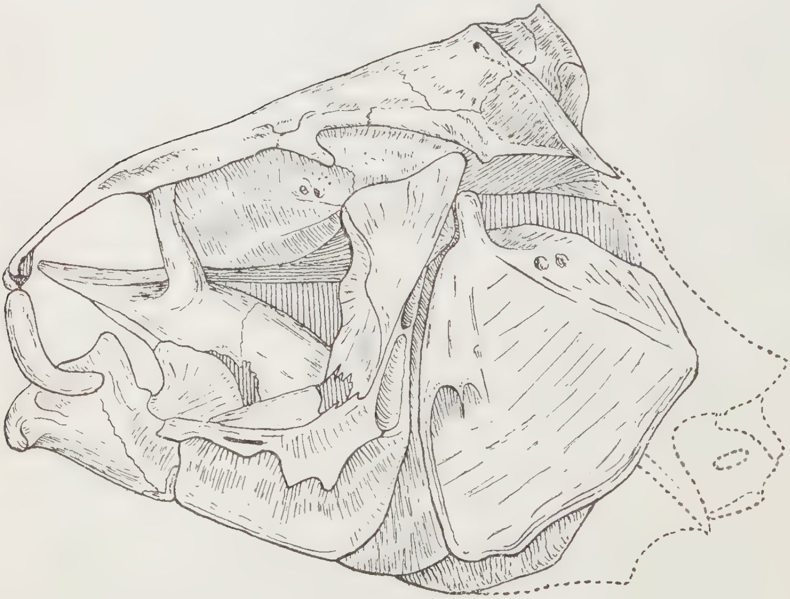


Fig. 80. *Eigenmannia macrops* (Blgr.). Skull seen from the left side. After Gregory (1933), fig. 73 A on p. 188.

suchlike. Those cases wherein the distance to the quadratum-articulare joint is very much larger, concern † *Acentrophorus*, with a relatively small mouth (pp. 85, 125, 421), *Distichodus langi* Nichols & Griscom with a very short mouth (p. 184), *Eigenmannia macrops* Blgr. with a small mouth (p. 186) (see my fig. 80), whereas it is rightly said of the allied *Electrophorus* (*Gymnotus*) *electricus* (L.) that it possesses a relatively large mouth (p. 187). These examples may suffice, it serves no purpose to collect further information of GREGORY's on the size of the mouth in such general terms as "small", "rather large" *etc.*

Also from the pictures, which are to be found in such large numbers in GREGORY, we cannot, however exact they are, draw any conclusions, unless we do so with the utmost reserve. The situation of the point, where, in the picture, the lower edge of the new upper jaw crosses the lower jaw, may have been influenced by 1. the condition in which the skull was dried, which may have made a displacement possible; 2. the degree in which the mouth is opened, which certainly influences the situation of the lower end of the maxillare with regard to the lower jaw; and 3. the degree of protrusion in those species which show protrusility of the mouth.

Notwithstanding all these difficulties we want nevertheless to try and show, with the aid of a number of pictures in GREGORY (1933) a number of cases where the new upper jaw crosses the lower jaw rostralward of the quadratum-articulare joint, in the sense mentioned above. For this intersection also occurs in Mammalia, where a processus coronoideus reaches far upward and projects above the level of the lower edge of the new upper jaw. Conditions like those in the higher Vertebrata may also be expected to be found in Pisces, where the caudal part of the lower jaw shows a projection or has been heightened. But we do not mean those cases when we speak about the intersection of the new upper jaw and the lower jaw; we only mean those cases where the slit of the mouth has been shortened in a clear, and fundamentally different way, more strongly than in the case in the higher Vertebrata, such as *e.g.* the Reptilia and the Mammalia. This condition, diverging for Pisces, is brought about by the fact that the new upper jaw caudally ends freely without being attached, either directly or indirectly, to the region of the quadratum.

If, then, with all these reservations we want to discuss a number of pictures in Gregory (1933) which might be included among the second diverging condition mentioned by us, we want to divide these cases into three groups, dependent on the line of the lower edge of the new upper jaw running in a rostroventral direction from the quadratum-articulare joint, or approximately through it, or on this line ending dorsal of the quadratum-articulare joint.

In the first group of cases the lower edge of the new upper jaw runs in such a way that this line lies rostroventrally of the quadratum-articulare joint. Only when certain conditions have been fulfilled, we may suppose that we have to deal with circumstances different from those met with in Vertebrata where it is also possible for a projection of the lower jaw to cross the new upper jaw, because here, too, the lower edge of the new upper jaw, when lengthened, crosses the lower jaw rostralward of the joint of the jaw, which is in many cases situated more dorsally, due to an angulus mandibulae.

These special conditions have been fulfilled if the new upper jaw is very short in comparison to the lower jaw. If then the new upper jaw, or at least its most backward part spreads in the direction of the lower jaw and crosses it, we have, in my opinion to deal with the second diverging condition, mentioned above. As examples we might mention *Gnathonemus curvirostris* Blgr. (fig. 63) (see my fig. 66), *Ictalurus punctatus* (Raf.) (fig. 78 A), *Cromeria nilotica* Blgr. (fig. 49) and *Aulostomus maculatus* Val. (fig. 104).

If the new upper jaw is relatively long in comparison to the lower jaw, we may only in special cases suppose that we might have to deal with the second diverging condition mentioned above. We can arrange those cases under four headings.

Under the first heading we mention *Eigenmannia macrops* Blgr. (fig. 73 A) (see my fig. 80), which forms a transition to the cases with a very short upper jaw, treated above. In *Eigenmannia* the lower edge of the new upper jaw runs namely exactly as it does in skulls with a relatively very short upper jaw, toward the rostral side of the lower jaw but then the new upper jaw takes a caudalward turn.

Under the second heading we mention those cases where the element forming the entire lower edge of the new upper jaw, is itself bent towards the rostral side of the lower jaw, in its caudal part. We find this beautifully illustrated in *Tautogolabrus adspersus* (Walbaum) (figs 129, 283 K) (see my fig. 81), less beautifully in

Pomacanthus arcuatus (L.) (figs 154, 290 A), while the picture of *Nexilosus albemarleus* Heller & Snodgrass (fig. 127) and of *Capros aper* (L.) (fig. 149 A) show this state when the mouth is wide open. We find this condition to a very slight degree in *Hippoglossus*, because here the bending in the lower edge of the new upper jaw approaches a gradual, continuous curve (figs 224, 225).

Under the third heading we mention those cases where the lower edge of the new upper jaw is formed by the two elements, but where the share of the maxillare forms a right or slightly obtuse angle with the share of the praemaxillare, so that the direction of the lower edge of the new upper jaw is clearly changed by this. This is very clearly the case in *Gymnarchus niloticus* Cuv. (fig. 62 B) (see my fig. 82), *Mormyrops deliciosus* (Leach) (fig. 62 A), *Gobiesox* (fig. 249) and in *Anarhichas* (fig. 255). It is less clearly visible in *Anableps tetrophthalmus* Bl. (fig. 98) (see my fig. 40). This is connected with the more obtuse angle between the lower edges of the two elements, which together form this lower edge. The size of this angle in *Astroscopus y-graecum* (C. & V.) (fig. 247) (see my fig. 42) makes this case less clearly fit this heading. A second cause of its slighter clarity is the phenomenon that the share of the maxillare in the formation of the lower edge of the new upper

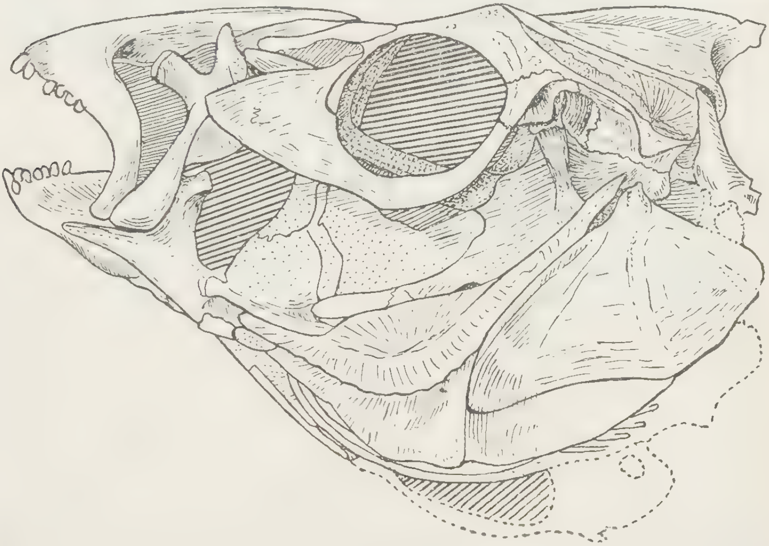


Fig. 81. *Tautogolabrus adspersus* (Walbaum). Skull seen from the left side. After GREGORY (1933), fig. 129 on p. 255.

jaw is, as a whole, very small. As examples of this we may mention *Gasterosteus spinachia* L. (fig. 103), *Hoplegnathus* (fig. 124), *Triacanthus* (fig. 160), *Pterois* (fig. 205) and *Callionymus* (fig. 242).

Under the fourth heading we mention those cases where the lower edge of the new upper jaw is straight and runs in the direction of the lower jaw, intersecting it in such a way that, in all probability, we have not to deal with conditions as we know them in the higher Vertebrata. We mention in this connection the picture of *Brama rayi* (Bl.) (fig. 182) (see my fig. 83) and that of *Percis nebulosa* Q. & G. (fig. 236 B), wherein the caudoventral edge of the maxillare even reaches across the lower edge of the lower jaw. It may, however, be asked if it is the natural situation that is represented here or if displacements of the free, loose end of the new upper jaw have taken place. *Alepocephalus rostratus* Risso (fig. 51), *Mastacembelus* (fig. 233), *Oneirodes* (fig. 279) and *Coryphaenoides* (fig. 262) with their relatively short upper jaws, which cross the lower jaw halfway, perhaps also belong under this fourth heading, as may *Petrocephalus bane* (Lac.) (fig. 64) (see my fig. 88). It is, however, quite well possible that these cases too, if the mouth were wide open, would prove not to differ fundamentally from conditions in the higher Vertebrata, in the sense that no shortening of the slit of the mouth is combined in a special way with the formation of a more rostrally situated corner of the mouth. When we consider the pictures in Gregory which show the skull with a very wide open mouth, the lower edge of the new upper jaw practically always intersects the lower jaw

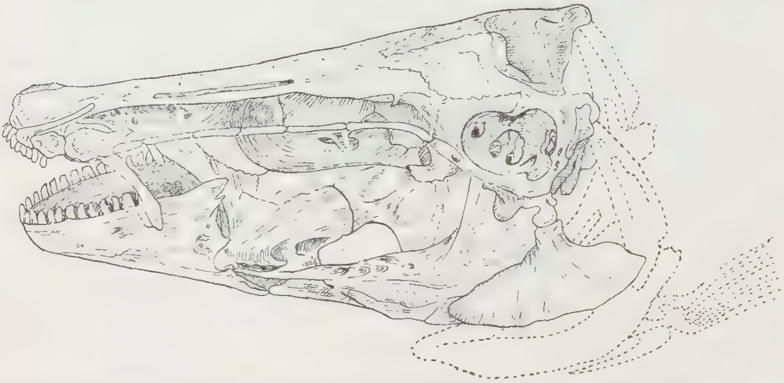


Fig. 82. *Gymnarchus niloticus* Cuv. Skull seen from the left side. After Gregory (1933), fig. 62 B on p. 170.

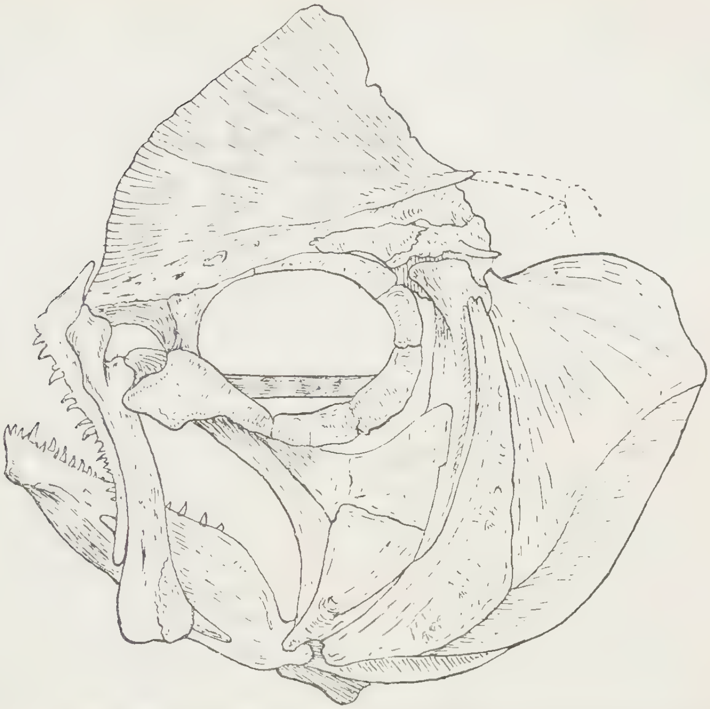


Fig. 83. *Brama rayi* (Bl.). Skull seen from the left side. After Gregory (1933), fig. 182 on p. 305.

just rostrally of, or in the caudally situated projection or the caudal elevation on the lower jaw. So here we have to deal with a condition which is characteristic of the higher Vertebrata. If we then, with many reservations, yet put the possibility, that in some cases, with a very wide open mouth a condition is present which is fundamentally different from that in the higher Vertebrata, and which might be brought under our fourth heading, we point out the pictures of *Lophodolos* (fig. 274) and also of *Zeus japonicus* C. & V. (fig. 148), where the lower edge of the new upper jaw crosses the lower jaw at a clear distance before the caudal elevation or processus on the lower jaw, further the picture of *Pelor* (fig. 206) (see my fig. 124), which shows practically no elevation on the lower jaw, but where the intersection of the lower edge of the new upper jaw and the lower jaw has a relatively very rostral situation; and for the same reason *Arapaima gigas* (Cuv.) (fig. 59) also belongs, perhaps, under the fourth heading, although a well developed processus is present on the lower jaw on the level of the intersection with the lower edge of the new upper jaw. Resuming, we may say that clear cases of the fourth heading are not known, in fact, we must perhaps conclude that this entire class is dubious. We can only be sure of the three first headings of our first group of cases, in which group the line of the lower edge of the new upper jaw runs rostroventral of the quadratum-articulare joint.

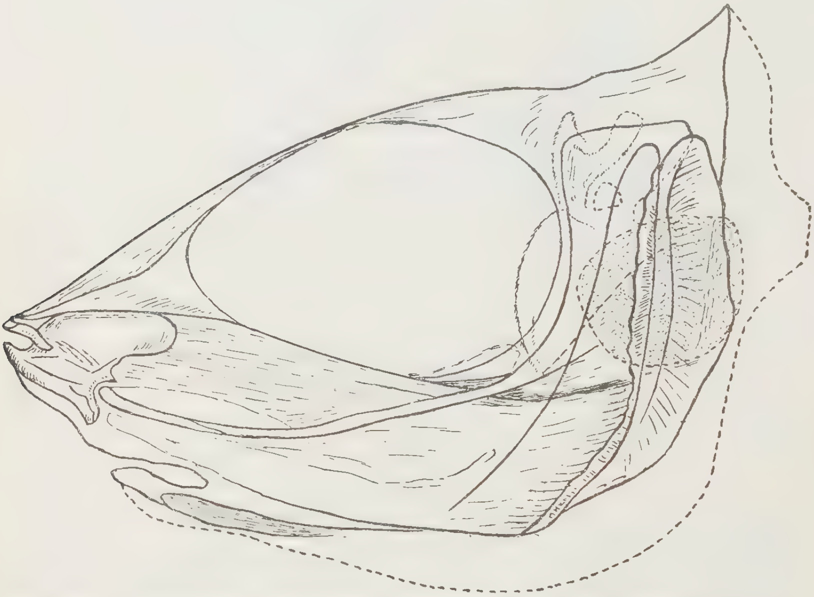


Fig. 84. *Opisthoproctus.* Skull seen from the left side. After GREGORY (1933), fig. 43 on p. 150.

In the second group the line of the lower edge of the new upper jaw runs, roughly, through the quadratum-articulare joint. In this case we observe, all the same, a shortening of the slit of the mouth combined with the formation of something like a secondary corner of the mouth, where the lower jaw is heightened far rostralward, and this rostral elevation of the lower jaw crosses the lower edge of the new upper jaw. This condition occurs in *Opisthoproctus* (fig. 43) (see my fig. 84), where the new upper jaw is relatively very short, and in *Exocoetus evolans* L. (*Halocypselus evolans*) (fig. 101) (see my fig. 27).

In the third group the line of the lower edge of the new upper jaw runs in such a way that it ends dorsal of the quadratum-articulare joint. Here too, we find, all the same, a shortening of the slit of the mouth, combined with the formation of something like a secondary corner of the mouth, where the lower jaw is heightened far rostralward, and this rostral elevation of the lower jaw crosses the lower edge of the new upper jaw. This condition occurs in *Dorosoma erebi* Gthr (*Chatoëssus erebi*) (fig. 39) (see my fig. 29), *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*) (fig. 66) (see my fig. 64), *Plecostomus commersonii* (Val.) (fig. 80) and *Mola mola* (L.) (fig. 172). It cannot be said whether *Phyllopteryx foliatus* (Shaw) (fig. 106), which is pictured with a wide open mouth, belongs to the second or the third group mentioned above, because, with a wide open mouth, the mutual situation of new upper jaw and lower jaw is so entirely different.

As a third diverging condition, wherein the new upper jaw of the higher Pisces differs from that of the higher Vertebrata we mentioned already (p. 191) the fact that the new upper jaw, by its toothlessness and its shape makes the impression of not having the function of a jaw. Here, too, the new upper jaw might have another function *e.g.* to border the gape. A number of phenomena, which we learnt in the above, such as the caudalward continuation of the maxillare, the part played by the elements of the new upper jaw in the shortening of the slit of the mouth, the caudal free ending of the loose end of the new upper jaw, which makes a strong function as a jaw impossible, all point to the function to border the gape, or anyway to functions different from that of a jaw. As a third diverging condition there are some other phenomena which must be discussed, such as the toothlessness, and certain peculiarities of shape of the new upper jaw.

Toothlessness in itself does not plead against the original function of the jaw, as we see in Aves and Testudinides. Neither does the presence of teeth in itself argue the existence of this function, as we see in *Coila nasus* Temm. Schl. (p. 147, fig. 41) (see my fig. 77) where the teeth occur on the maxillare beyond the quadratum-articulare joint, at least if the cause of the denticulate character is the presence of real teeth. One might be inclined to regard cases, where the row of teeth in the new upper jaw reaches very far backwards from the same point of view; as a matter of fact they continue as far as close to the quadratum-articulare joint, so that, with a closed mouth, the most caudal upper-jaw-teeth lie lateral of the lower jaw. This condition is pictured for † *Cheirolepis trailli* Agassiz (figs 12 A, 286 A) (see my fig. 95), for † *Pholidophorus macrocephalus* Agassiz (fig. 29), *Engraulis encrasicholus* (L.) (fig. 40) (see my fig. 76), *Gonostoma elongatum* Gthr (fig. 53), *Stomias boa* (Risso) (fig. 56), *Osteoglossum* (fig. 57) (see my fig. 116), *Brycon dentex* Gthr (fig. 70), *Omosudis lowii* Gthr (fig. 89), *Scopelarchus anale* (Brauer) (fig. 90), *Evermannella atrata* (Alcock) (fig. 91), *Microspathodon chrysurus* (C. & V.) (fig. 128), and *Melanonus* (fig. 260). But the few pictures of such new upper jaws, which have been drawn with wide open mouth, such as *Chauliodus sloanei* Bl. Schn. (fig. 55) and *Gastrostomus* (fig. 94) (see my fig. 87), show us that, also in those cases, all the teeth of the new upper jaw, the most backward ones included, may serve as elements to catch or hold the food. The toothlessness of the maxillare does not prove anything for our purpose in the cases where the maxillare is excluded from the gape (Gregory, 1933, pp. 193, 204, 219, 220, 223), a process which has begun by the reduction of the maxillare and the predominance of the praemaxillare (Gregory, 1933, pp. 187, 204, 219), so that there are all sorts of transitional stages.

For an insight in an other function of the praemaxillare and the maxillare, only those cases where teeth partly or entirely are lacking in the free lower edge of the new upper jaw, whereas they do occur in the lower jaw, are of importance. Sometimes the lower edge of both maxillare and praemaxillare are quite toothless as is the case in *Astroscopus* (fig. 247) (see my fig. 42) (*n.b.* in *Rhynchoceratias* praemaxillare and maxillare are toothless, too, but here there are no teeth in the lower jaw either; see fig. 281; see my fig. 63). In an other case the entire lower edge of the new upper jaw is toothless too, but this lower edge is formed by the praemaxillare only; this occurs in *Lophodolos* (fig. 274). Then, the entire lower edge of the new upper jaw may be formed by the praemaxillare, whereas this is only toothless as far as the caudal part is concerned, as is the case in *Lestidium speciosum* Bellotti (fig. 88). In many cases where the maxillare is entirely or partly situated in the free lower edge of the new upper jaw, behind the praemaxillare, the free lower edge of the entire maxillare, as well as the caudal part or the caudal point of the praemaxillare, is toothless, as is the case in *Distichodus langi* Nichols & Griscom (fig. 71), *Cottus octodecimspinosus* (Mitchill) (fig. 212), *Aspicottus (Enophrys)* (fig. 216), *Hippoglossus* (fig. 224), *Cottoperca gobio*

Gthr (fig. 239 A), *Gobiesox* (fig. 249), *Anarhichas* (fig. 255), *Fierasfer* (fig. 257) (see my fig. 146), *Lota* (fig. 258 B), *Coryphaenoides* (fig. 262) and *Opsanus* (fig. 263). Finally, in a number of cases the lower edge of the maxillare is quite toothless whereas the praemaxillare, situated before it, is, judging from the lateral view in the picture, quite covered with teeth; we find this in *Alepocephalus rostratus* Risso (fig. 51), *Gymnarchus niloticus* Cuv. (fig. 62) (see my fig. 82), *Petrocephalus bane* (Lac.) (fig. 64) (see my fig. 88), *Electrophorus electricus* (L.) (fig. 73 B), *Esox masquinongy* Mitchill (fig. 95) (see my fig. 30), *Scorpaena scrofa* (L.) (figs 116, 203) (see my fig. 79), *Trigla* (fig. 219) and *Periophthalmus* (fig. 228) (see my fig. 41). All these cases of entire or partial toothlessness, whereas the lower jaw does show teeth, point to the fact that, at any rate these parts of the new upper jaw might lack the function of jaw.

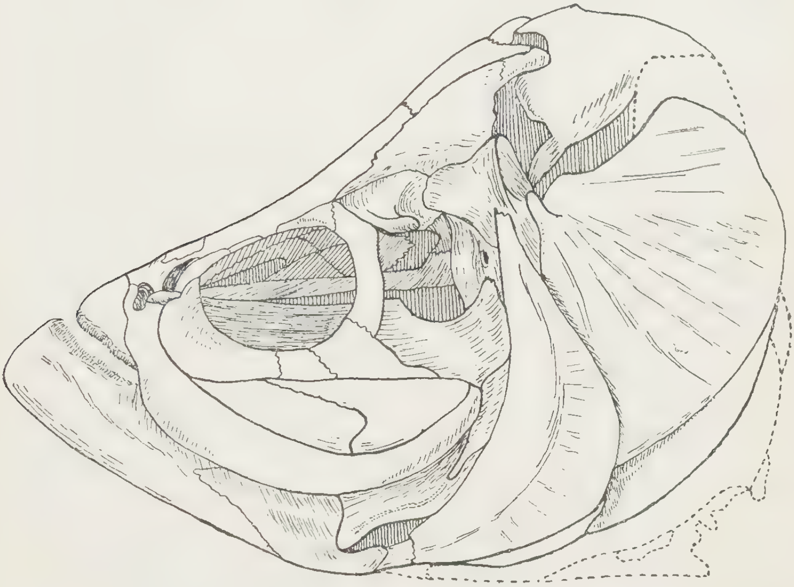


Fig. 85. *Tarpon atlanticus* (C. & V.). Skull seen from the left side. After Gregory (1933), fig. 31 on p. 139.

Certain peculiarities of shape also argue in favour of the idea of the new upper jaw having no jaw function, or not only having a jaw function such as we know it in the higher Vertebrata.

In the first place we point out the phenomenon that the free lower edge of the new upper jaw shows, on the ventral side, a convex edge, which is not combined with a curve in the lower jaw in the corresponding place; as a rule this part of the new upper jaw shows, as a whole, a garland-like character, when this convex lower edge occurs. This phenomenon is beautifully developed in *Tarpon atlanticus* (C. & V.) (fig. 31) (see my fig. 85), less beautifully but yet very clearly it may be found in † *Leptolepis dubius* (Blainville) (figs 30, 288 A), *Chanos chanos* (Forsk.) (*Chanos salmoneus*) (fig. 44) and in other constellations in *Belonesox belizanus* Kner (fig. 96). In all these cases this convex curve is formed by the toothless maxillare. This convex curve occurs in a very slightly pronounced way in *Petrocephalus bane* (Lac.) (fig. 64) (see my fig. 88) and *Diodon hystrix* L. (fig. 170) (see my fig. 121), where in both cases this convex curve is formed by the toothless maxillare, and in *Exocoetus evolans* L. (*Halocypselus evolans*) (fig. 101) (see my fig. 27), where it is formed by the toothless praemaxillare. Even in the composite diagram based on the study of the skulls of about fifty species of Teleostei given by GREGORY (1933, fig. 7) (see my fig. 114) the maxillare is pictured, lying in the caudal part of the free lower edge of the new upper jaw, with a slightly convex toothless lower edge, which, when the mouth is closed, hangs laterally by the side of the lower jaw. Yet, from the shape of part of or the entire free lower edge of the new upper jaw, it may only be concluded with reservations, that part or the whole of it has no jaw function. A number of cases are *viz.* pictured where this convex lower edge is covered with teeth; in this connection we mention † *Pholidophorus macrocephalus* Agassiz (fig. 29) and † *Ichthyodectes serridens* Smith Woodward (fig. 35). In *Chirocentrus dorab* (Forsk.) (figs 34, 288 C) only the most caudal part of the free lower edge of the maxillare is convexly bent, at the same time this part is toothless.

In the second place, as regards peculiarities of shape of the new upper jaw, causing it to make the impression that it has no ordinary jaw function, we point out some very peculiarly shaped elements of the new upper jaw, added to which the free lower edge of the new upper jaw shows a very peculiar shape, too. I am referring to conditions in *Cromeria nilotica* (Blgr.) (fig. 49), *Gnathonemus curvirostris* Blgr. (fig. 63) (see my fig. 66), *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*) (fig. 66) (see my fig. 64), *Distichodus langi* Nichols & Griscom (fig. 71), *Plecostomus commersonii* (Val.) (fig. 80 A), *Zanclus cornutus* (L.) (fig. 158) (see my fig. 117) and *Luvarus imperialis* (Raf.) C. & V. (fig. 185), to mention only some striking examples. Among them are a number of cases, of which we heard before, in the discussion of the phenomenon, that, perhaps in those cases, the function of the new upper jaw is to border the gape. In this connection we also discussed many other cases such as the peculiarities of a new upper jaw which is very small in proportion to the lower jaw; the free lower edge of the new upper jaw which is bent, either with the convex or the concave side pointing downward; the cases where the praemaxillare and maxillare make a nearly right or slightly obtuse angle, *etc.* Closely related to this latter case is also the peculiar shape of the maxillare in *Hydrocyon lineatus* Blkr (fig. 69) (see my fig. 86) and *Periophthalmus* (fig. 228) (see my fig. 41) as compared to *Anarhichas* (fig. 255) and such like cases already discussed.

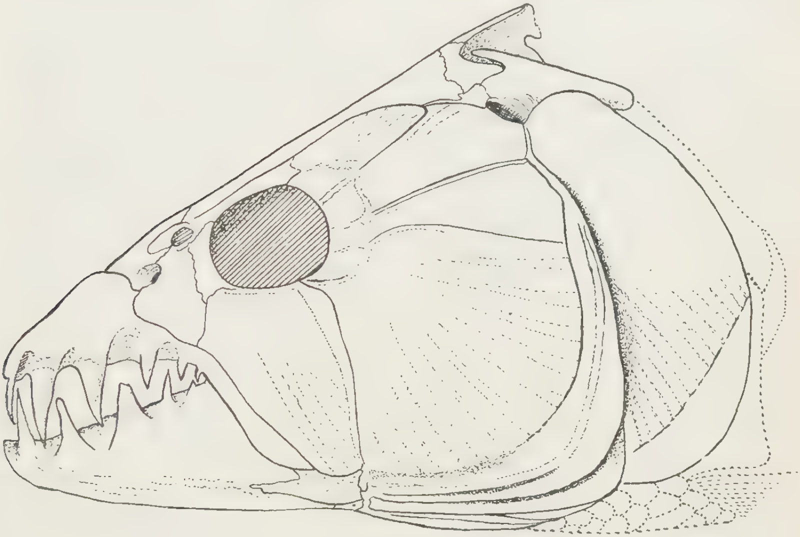


Fig. 86. *Hydrocyon lineatus* Blkr. Skull seen from the left side. After GREGORY (1933), fig. 69 on p. 184.

Finally we point out those cases where the maxillare hardly if at all takes part in the free lower edge of the upper jaw, and does not lie against the praemaxillare either, but is situated at a clear distance, and entirely separated, so that, also in those cases there is evidently no question of a normal jaw function of the maxillare. This condition probably occurs in *Cheilodactylus spectabilis* Hutton (fig. 136) and in *Pomatomus saltatrix* (L.) (fig. 177).

So, in the preceding pages we have come to know numberless sorts of cases, where the new upper jaw shows, entirely or partially, no normal jaw function, or where such a function is uncertain. For a sure judgment, more data would be needed. As long as they are lacking we shall have to abstain from making a difference between new upper jaws which do, and those which do not have the normal functions of jaws, and until then we shall have to accept the new upper jaw in its morphological and not in its functional aspect, which really forms the subject of this paragraph.

Before passing to this, however, we want to make some observations on new upper jaws in the higher Pisces, which, in our opinion may be compared with those of the higher Vertebrata.

One will, in the first place, be inclined to compare to the new upper jaws of the higher Vertebrata, those cases where the free lower edge of the new upper jaw is furnished with teeth. But in the above we already saw that teeth may also occur caudal of the quadratum-articulare joint. For the rest, the presence of teeth by itself does not necessarily mean that they serve to seize, hold or cut up the food or prey. A jaw function seems very probable to me, if a series of well developed teeth grows in the new upper jaw practically as far as the quadratum-articulare joint, which cases were mentioned above. A jaw function is also probable, if the new upper jaw runs either in the direction of the quadratum-articulare joint, or dorsal of it, but finishes at a more or less far distance rostrally from this joint, while the free edge of the upper jaw is entirely or for the greater part furnished with teeth. (In my opinion, we may not decide that a jaw function exists if the line of the lower edge of the new upper jaw runs to a spot clearly rostral of the quadratum-articulare joint.) I should like to conclude to a probable jaw function in the following cases, where the line of the lower edge of the new upper jaw runs in the direction of the quadratum-articulare joint; the examples being arranged according to the decreasing relative length of the part of the new upper jaw furnished with teeth in proportion to the distance of the point of the snout to the quadratum-articulare joint: *Coryphaena hippurus* L. (fig. 183), *Sphyraena barracuda* (Walbaum) (fig. 141), *Seriola zonata* (Mitchill) (fig. 179), *Electrophorus electricus* (L.) (fig. 73 B), *Scorpaena plumieri* Bl. (fig. 201), *Lachnolaimus maximus* (Walbaum) (fig. 130) (see my fig. 129) and *Chaetodipterus faber* (Brouss.) (fig. 152); in all these cases it is the praemaxillare which bears the teeth. I should also like to conclude to a probable jaw function in the following cases, where the line of the lower edge of the new upper jaw runs dorsal of the quadratum-articulare joint; the examples being arranged according to the decreasing relative length of the part of the new upper jaw furnished with teeth in proportion to distance of the point of the snout to the quadratum-articulare joint: *Iniistius* sp. (fig. 132) (see my fig. 128), *Cheilodactylus* (fig. 136) and *Sphyraena* (fig. 284).

The decision whether a jaw function is present, is very difficult when the new upper jaw is entirely, or for a considerable part, toothless. It may be present in the following two cases: first when the new upper jaw runs toward the quadratum-articulare joint which it practically reaches and secondly when the new upper jaw is shorter but runs in a direction dorsal of the quadratum-articulare joint and the lower jaw remains low over its full length, so that the new upper jaw does not help to form a secondary corner of the mouth. As examples of the first case, wherein the entirely, or to a considerable degree toothless new upper jaw reaches nearly as far as the quadratum-articulare joint, we mention a.o. † *Platysomus* (figs 15 B, 286 D) (see my fig. 90), † *Perleidus* (figs 21 A, 283 C, 286 C), *Cetomimus regani* Zugmayer (fig. 92), *Myctophum humboldti* (Risso) (fig. 93), *Fundulus* (fig. 96 A), *Haemulon* (fig. 121) (see my fig. 127), *Spheroides stictonotus* (Temm. & Schl.) (fig. 167), *Antennarius* (figs 265, 288 D) and *Chaunax* (fig. 271). To this series also belongs *Aspicottus* (*Enophrys*) (fig. 216) which, notwithstanding this relatively strongly developed toothlessness combined with a caudally extended row of teeth in the lower jaw, yet shows, in my opinion, a jaw function in the development and structure of the new upper jaw.

As examples of the second case, wherein the entirely or to a considerable degree toothless new upper jaw does not reach close to the quadratum-articulare joint, because it is shorter, but where we may all the same attach jaw functions to this upper jaw, because it runs in a direction dorsal of the quadratum-articulare joint, and the lower jaw remains low over its entire length, so that the new upper jaw does not help to form a secondary corner of the mouth, we mention: *Polypterus* sp. (fig. 10), *Clarias* sp. (fig. 78 B), *Gerres lineatus* (Humboldt) (fig. 126) and *Anabas testudineus* (Bl.) (*Anabas scandens*) (fig. 145 B).

So, even if there are numerous cases where the new upper jaw of the higher Pisces may be compared to those of the higher

Vertebrata, we have before this, come to realize, that, in numerous cases this comparability is doubtful, and that, when more data are lacking we must refrain from making such a distinction between new upper jaws which do and those which entirely or in part do not have proper jaw functions. So, in discussing the size of the upper jaw, we shall have to take the new upper jaw in its morphological sense, and not in the functional one. Of the size we shall first discuss the length, and then the measurements in other directions.

Of importance for the length of the new upper jaw in the higher Pisces, are the data given by GREGORY (1933) on the length of the gape, the length of the mouth, and the length of the jaws.

GREGORY (1933) defines the gape with the aid of the line of the gape, *i.e.* the line from the quadratum pivot (that is the midpoint of the articular hinge of the quadratum) either towards the prosthion (that is the most anterior point of the snout), or towards the praemaxillon or premaxillary tip (that is the most anterior point of the praemaxillare in the norma lateralis; these two most anterior points often coincide) (p. 420). For the rest, the meaning of the idea "gape" in GREGORY, can also be derived from his observation that a positive displacement of the projection of the quadratum pivot (*i.e.* the mid-point of the articular hinge of the quadratum) upon the horizontal will lengthen the gape, a negative displacement of this projected point will shorten the gape; the horizontal being the line joining the prosthion and the pygidion (the prosthion is the most anterior point of the snout; the pygidion is the mid-point of the narrowest part of the caudal peduncle) (p. 420). So these definitions entail that the length is determined as far as the joint of the jaw, so it is the length of the old upper jaw. In the definition based on the projection upon the horizontal, however, the slope of the upper jaw should be counted in, to have a measure for the length of the jaw, for the projection of a short, slightly sloping upper jaw may be as large as that of a long one with a pronounced slope. For certain Scaridae, where an ascending process of the dentale is attached to the maxillare, GREGORY (1933, p. 258) observes that thus the gape of the mouth was reduced (see my fig. 78). In this case "gape" is identical to the length of the jaw as far as the secondary corner of the mouth. So we must take into account the fact that "gape" has this latter meaning, also in analogous cases among the higher Pisces. Further we yet mention, that, according to GREGORY (1933, p. 418) lengthening of the jaw is accompanied by an increase in the length of the gape. In GREGORY this refers to the length of the old upper jaw as far as the quadratum-articulare joint, but it also holds good for the length of the new upper jaw as far as the secondary corner of the mouth.

The size of the mouth is also connected with the length of the upper jaw. As GREGORY says (1933, p. 416) the mouth will increase in size when the jaw bones have lengthened, furthermore, small mouths will be caused by progressive reduction of the normal jaws of a predaceous type, with accompanying reduction of the dimensions of the jaws. So the size-indication of the mouth also refers to the length of the old upper jaw as far as the quadratum-articulare joint. All the same we shall collect these data in GREGORY, too.

The upper jaw of moderate length in the predaceous mouth is normal in Pisces; all conditions in Pisces have evolved from this primitive condition (GREGORY, 1933, pp. 416, 431). *Salmo* (see my fig. 18) and the typical Esocidae (see my fig. 30), Enchodontidae and Iniomi show such a normal predaceous mouth (p. 416; on p. 204, however, it is said of one of the Iniomi that the mouth is large). Thus, *Anguilla chrysypa* Raf. (*Anguilla rostrata*) shows, with predaceous adaptation, a moderate length of the jaws (p. 203). In all these genera and groups, the new upper jaw forms a very important part of the distance from the front point of the snout to the quadratum-articulare joint, judging from the pictures given. Opposed to these, however, are the following remarks by GREGORY. He calls † *Cheirolepis* a primitive palaeoniscoid Actinopterygian, and yet it has large jaws and also a large maxillare (pp. 85, 112, 421) (see my fig. 95). Further on (p. 421) GREGORY says that the Teleostei appear to have been derived from small-mouthed forms. Thus it is highly probable that in the primitive Carangidae the mouth is small whereas those with more predaceous habits show larger mouths, as in *Trichiurus* (p. 302) where the new upper jaw takes up a considerable part of the upper edge of the mouth. Thus, in *Aspius aspius* (L.) (*Aspius rapax*) with its predatory habits, the jaws are much larger than in the typical carp mouth of *Cyprinus carpio* L. *c.s.* (GREGORY, 1933, p. 193). GREGORY (p. 123) also mentions with regard to the † Protospondyli, that it is not sure whether they are descended from large-mouthed palaeoniscoid ancestors; the oldest † Protospondyli known are small-mouthed.

From these normal predaceous mouths, from these small-mouthed † Protospondyli and Teleostei are derived on the one hand the very large mouths with elongated upper jaws, on the other hand the very small mouths with shortened upper jaws (Gregory, 1933, pp. 123, 125, 416, 421, 431).

To this line of development in the direction of the large mouths and the very long upper jaws belongs, as an extreme case, *Gastrostomus*, with its enormous mouth with an immense cavernous opening and with enormously long jaws, which, according to the picture, are formed by the rod-like new upper jaw (Gregory, 1933, pp. 212, 213, 416, fig. 94) (see my fig. 87). Also in *Melanocetus polyactis* Regan the jaws are enormously deep; the new upper jaw sharing in this great length of the upper jaw (p. 405, fig. 272). Also *Lophius* shows an immense deepening of the mouth and enormous jaws, which are accompanied by a very great length of the new upper jaw (pp. 394, 416, fig. 267). A great elongation of the jaws and at the same time of the new upper jaw is also shown by *Lepisosteus* (pp. 127, 421) (see my fig. 65) and especially by *Tylosurus* with its excessive elongation of the jaws (pp. 221, 421/422, 453) (see my fig. 94). In this connection *Istiophorus*, with its great elongation of the new upper jaw, may be mentioned, too (pp. 316/317). Here is perhaps the best place to mention Böker's observation (1937, p. 24) that *Belone belone*

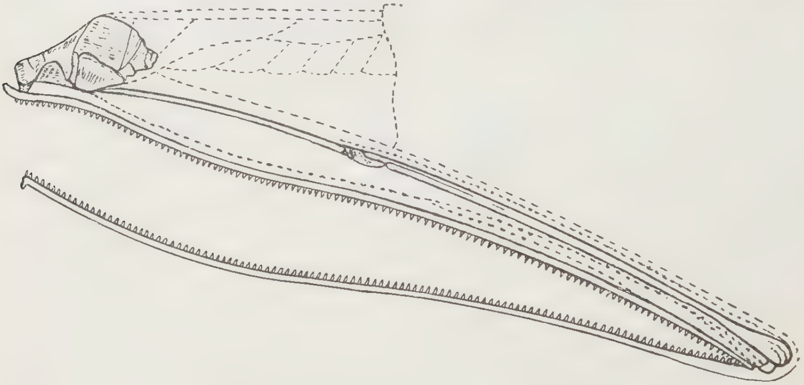


Fig. 87. *Gastrostomus*. Skull seen from the left side. After Gregory (1933), fig. 94 on p. 213.

(L.) possesses strongly elongated jaws as do also other related Scomberesocidae. Less long, but yet forming exceptions with regard to the normal Teleostei, according to GREGORY (1933, p. 422) are the backwardly lengthened jaws of Engraulidae, such as *Engraulis* with its long jaws (p. 147) (see my fig. 76) which is joined by *Coila* with its long jaws (p. 147) (see my fig. 77), further among the Apodes genera such as *Lycodontis* with its posteriorly lengthened jaws (p. 203) (see my fig. 119), Gonostomidae, such as *Gonostoma* (fig. 160), Gastrostomidae (see my fig. 87), such as *Stomias* (fig. 162) and some others; in all mentioned genera it is the new upper jaw which forms this great length of the posteriorly lengthened mouth. For the rest GREGORY mentions a large mouth or long jaws in the following cases: the primitive Amioid † *Furo* (*Eugnathus*) with its long new upper jaw has a larger mouth than the primitive † Protospondyli (p. 85, fig. 27), then, † *Eurypholis* with its large mouth and long new upper jaw (p. 204, fig. 83), *Belonesox* with its enlarged jaws and its very long new upper jaw (pp. 218, 219, fig. 96 B), *Sphyraena*, where, as in the Esocidae and Muraenidae (Anguillidae) the jaws, and with them the new upper jaw have been lengthened by growing forward (p. 267, fig. 141), *Polynemus*, where the posterior end of the upper jaw and of the new upper jaw, runs far backward, whereby is produced a convergent resemblance to the jaws of primitive † Palaeoniscidae (p. 268), *Zeus* with its relatively large mouth and also relatively very long new upper jaw (p. 271, fig. 148), *Symbranchus* with its fairly long jaws, where the new upper jaw is also fairly long (p. 352, fig. 231) (see my fig. 123), *Percophis*, which represents a fairly large-mouthed predaceous type (p. 363) and *Antennarius* with its long new upper jaw and allied Pediculati with a large mouth (p. 390, fig. 265). To these may be added *Polyodon*, of which the primary jaws are very large, which length is, according the picture, shared by the new upper jaw (p. 117, fig. 17). An other cause of the enlargement of the maxillare perhaps occurs in *Polypterus*, where the maxillare has apparently invaded the territory of the suborbital series; there is, however, also an opinion that some suborbital elements have been added to this maxillare (GREGORY, 1933, p. 110).

In the opposite line of development, going in the direction of the shortened upper jaw, we find as an extreme case the extremely minute nibbling mouth in certain Mormyridae, such as *Gnathonemus* with its minute mouth, where the new upper jaw is extremely short, too (pp. 171, 417, fig. 63) (see my fig. 66) and certainly also *Petrocephalus* (pp. 171–173, fig. 64) (see my fig. 88). The condition in *Rhamphichthys rostratus* (L.) with its very small mouth recalls somewhat the form in certain Mormyridae (p. 189). Very short jaws, in which the new upper jaw shares, also occur in Balistoidei, such as Acanthuridae, the genus *Xesurus*, the small-mouthed Teuthidae, Zanclidae (see my fig. 117) and Balistidae

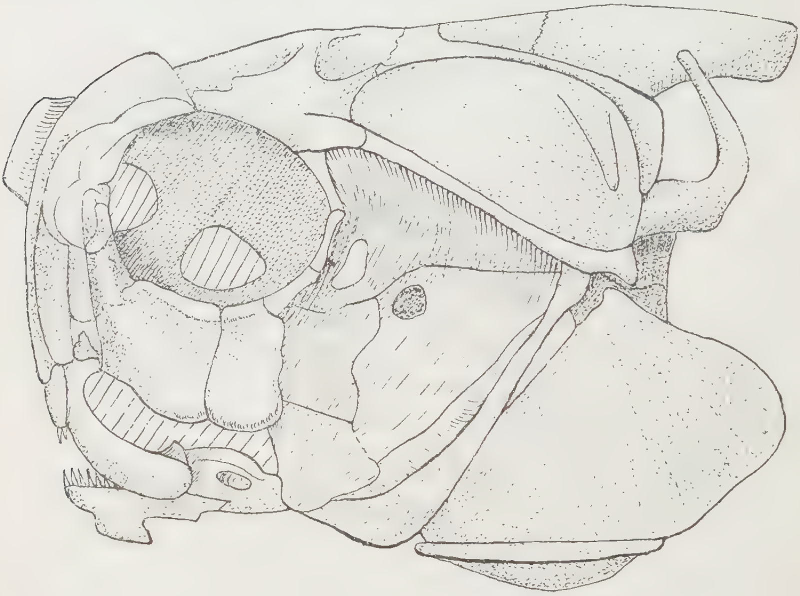


Fig. 88. *Petrocephalus bane* (Lac.). Skull seen from the left side. After GREGORY (1933), fig. 64 on p. 172.

(see my fig. 43) with *Alutera* (see my fig. 91) and the Plectognathi (pp. 281/282, 288/289, 290, 416, 422, 438, fig. 290). Also in Chaetodontoidei as in *Pomacanthus* and *Chaetodon*, the upper jaw is very short (pp. 281/282, 416, 422, fig. 290). GREGORY (1933, p. 416) mentions, together with Balistoidei and the Chaetodontoidei, some other groups showing a small mouth with a shortened jaw, *viz.* the Sparidae, Hoplegnathidae, Cichlidae, Pomacentridae, Labridae and Scaridae. Also in a few other Percoidei, *viz.* in *Priacanthus* the mouth is fairly short (p. 247) and in *Cheilodactylus spectabilis* Hutton the jaws are very short (p. 260). *Fundulus* with its small mouth has been derived from the less minute mouths of the type seen in the Umbridae with their fairly small mouths (pp. 216, 416). The case is the same for the later genera of the Semionotidae, such as † *Dapedius*, † *Semionotus*, † *Lepidotus*, *c.s.* which show a marked shortening of the jaw as compared to the older genera (p. 125). In † Catopteridae of the Triassic with a fair-sized mouth, we have also evidence that a short or moderate mouth has been derived from a large mouth (p. 116). Also in Oncocephalidae the mouth parts are relatively small and apparently have been derived by reduction from a more normal condition (p. 399). We conclude these data with some observations, derived from GREGORY (1933). According to him the jaws, also the upper jaw, are small and short and the mouth relatively small in *Exocoetus evolans* L. (*Halocypselus evolans*) (p. 221) (see my fig. 27), the jaws are short in Xenopterygii (p. 371), relatively short in *Serrasalmo* and *Hydrocyon* (p. 184) (see my fig. 86), the mouth is very small in *Anableps* (p. 220) (see my fig. 40), *Percopsis guttatus* Ag. (p. 232) and in *Tetrabrachium ocellatum* Gthr (p. 394). Finally GREGORY mentions a fairly small mouth in *Gasterosteus trachurus* C. & V. (p. 224), and a small mouth in *Gasteropelecus* (p.185), *Notacanthus* (p. 201), *Capros aper* (L.) (p. 272) and *Luvarus* (p. 306). Probably *Halosaurus* also belongs to these, although it is said, as opposed to *Notacanthus* that the mouth is moderate-sized (p. 201).

So far the data on the length of the new upper jaw, and what could be discussed in connection with it.

About the breadth, so the measurement in the transverse direction of the upper jaw of the higher Pisces, GREGORY (1933) says the following.

In *Plecostomus*, with its small, almost tadpole-like mouth, the width across the quadratum-articulare joints is about twice the length of the jaw itself; so this refers to the width of the old upper jaw; the maxillare has been reduced, and the praemaxillare is also relatively short (p. 196, fig. 80). In *Astroscopus* the opposite pterygo-metapterygoid tracts are removed far from the mid-line, which influences the distance between left and right new upper jaw (p. 369, figs 247, 248) (see my fig. 50). In *Fundulus*, *Tylosurus*, *Hemirhamphus* and *Halocypselus* the mouth is rather broad transversely (p. 223). In the whole Plectognath stock the jaws have greatly increased in breadth, and, to a less extent, in length (pp. 288/289). In *Lagocephalus* there is a transverse broadening of the enlarged and widened mouth (pp. 290, 292). In *Pelor japonicum* C. V. the mouth is broad (p. 329). In *Lophius* there is an immense widening of the mouth with an increase in the transverse diameter of the mouth (pp. 394, 396). Probably the breadth of the new upper jaw is also influenced by the differences in width of the head in the mostly wide-headed predatory Fishes, such as *e.g. Esox*, and the narrow-headed non-predatory Fishes, which feed on the lower small animals, as is the case with *Cyprinus carpio* L. Even within the species *Muraena anguilla* L. (*Anguilla vulgaris*) wide-headed forms are distinguished by the side of narrow-headed ones, which is also connected with the kind of food they take (Böker, 1937, pp. 53/54).

As regards the height of the upper jaw, we want to begin by pointing out that we must separately regard the high vertical development of the new upper jaw, due to the enlargement of the intergrown teeth into a so-called beak, such as occurs in *Hoplegnathus* (p. 250), the Scaridae (p. 257) (see my fig. 78), and *Lagocephalus* (p. 290). The information that the praemaxillare in *Fundulus*, *Tylosurus* (see my fig. 94), *Hemirhamphus* and *Halocypselus* is more or less beak-like (p. 223) must, judging from the pictures, be something else, and refer to the shape of the praemaxillare itself. *Acanthocybium* also shows a beak-like praemaxillare (p. 317). An other information on the vertical measurement of the new upper jaw, may be derived from the data on the thickness of the new upper jaw. A great thickness will generally mean that the upper jaw is also high in the vertical direction. Thus, according to Gregory (1933), the jaws in *Serrasalmo* and *Hydrocyon* are powerful, which refers especially to the praemaxillare, which is usually strong (p. 184, fig. 69) (see my fig. 86); in *Gasteropelecus* the jaws are stoutly built (p. 185) as they are in Xenopterygii (p. 371, fig. 249), in *Cheilodactylus spectabilis* Hutton the jaws are strong (p. 260, fig. 136). In *Archosargus*, with the most strongly built skull, the upper jaw shows a very great massiveness (pp. 249, 423; figs 123, 291 C) (see my fig. 89). This massiveness of the praemaxillare does not only occur in *Archosargus*, but also in other Sparidae showing the crushing type, such as in *Anarhichas* (p. 423, fig. 255). This information, that the Sparidae show a great enlargement of the maxillare and palatinum (p. 438), cannot but refer to the vertical measurement, for the jaws are short, as we saw in the above. Also in Oncocephalidae the arcus palatoquadratus is unusually massive, but this is apparently a secondary enlargement to support the massive neurocranium which rests upon it, for the mandible is delicate (p. 401) (see my fig. 67).

From the pictures given by Gregory (1933) we can derive several things regarding the vertical measurements of the new upper jaw, or perhaps we had better say, regarding the measurement perpendicular on the longitudinal axis of the new upper jaw. A high vertical measurement of the new upper jaw can be formed in different ways. A high new upper jaw where both the praemaxillare and the maxillare are high and situated entirely or for the greater part behind each other, are found a.o. in † *Platysomus parvulus* Williamson (figs 15 B, 286 D) (see my fig. 90), † *Portheus molossus* Cope (figs 36, 283 F, 288 B), *Gerres lineatus*

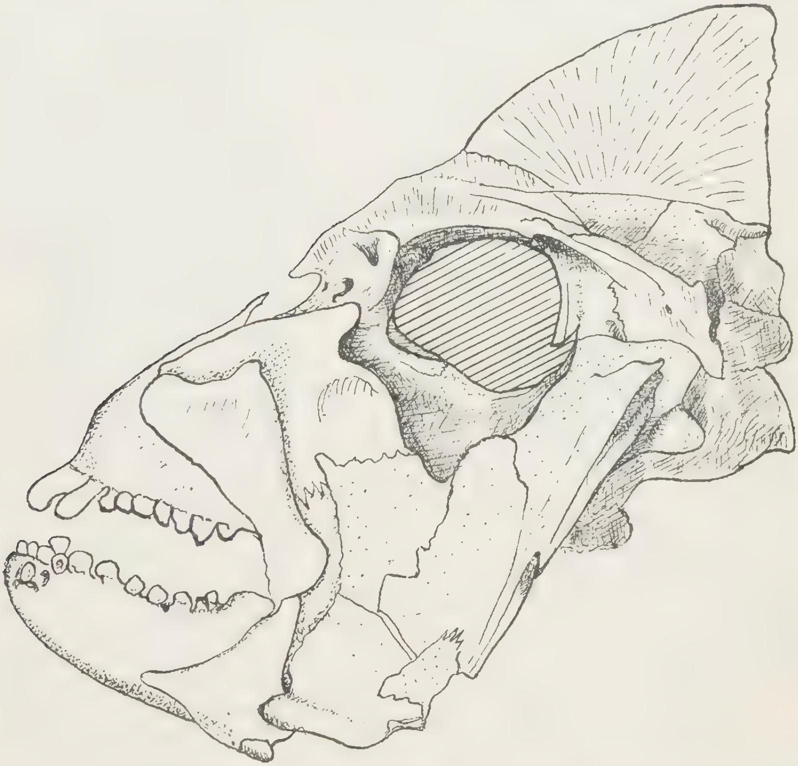


Fig. 89. *Archosargus probatocephalus* (Walbaum). Skull seen from the left side. After Gregory (1933), fig. 123 A on p. 249.

(Humboldt) (fig. 126), *Xesurus punctatus* (Gill) (figs 157, 290 B), *Zanclus cornutus* (L.) (fig. 158) (see my fig. 117), *Teuthis virgata* (C. V.) (fig. 159), *Triacanthus* (fig. 160), *Diodon hystrix* L. (fig. 170) (see my fig. 121), while *Scorpaena plumieri* Bl. (fig. 201), *Scorpaena scrofa* L. (figs 116 A, 203) (see my fig. 79) and *Pterois* (fig. 205) form a transition to the following case. – In other cases a great vertical height is namely reached by the praemaxillare and maxillare being situated, entirely or for the greater part, on each other, or running practically parallel to each other, as *e.g.* in *Aulopus* (fig. 85), *Anableps tetrophthalmus* Bl. (fig. 98) (see my fig. 40), *Myripristis murdjan* (Forsk.) (fig. 111), *Calamus* (fig. 122), *Tautogolabrus adspersus* (Walbaum) (figs 129, 283 K) (see my fig. 81), *Lachnolaimus maximus* (Walbaum) (fig. 130) (see my fig. 129), *Zeus japonicus* C. V. (fig. 148), *Capros aper* (L.) (fig. 149 A), *Spheroides stictonotus* (Temm. & Schl.) (fig. 167), *Seriola zonata* (Mitchill) (fig. 179), *Selene vomer* (L.) (fig. 181 A), *Trichiurus lepturus* L. (figs 195, 291 D), *Astroscopus* (fig. 247) (see my figs 42 and 50) and *Blennius* (fig. 252). – In yet other cases the size of the vertical height of the new upper jaw is due only to such a height of one of the two elements. The great height is caused by the praemaxillare only in *Belonesox belizanus* Kner (fig. 96 B), *Hoplegnathus* (fig. 124), *Balistes carolinensis* Gmel. (fig. 161) (see

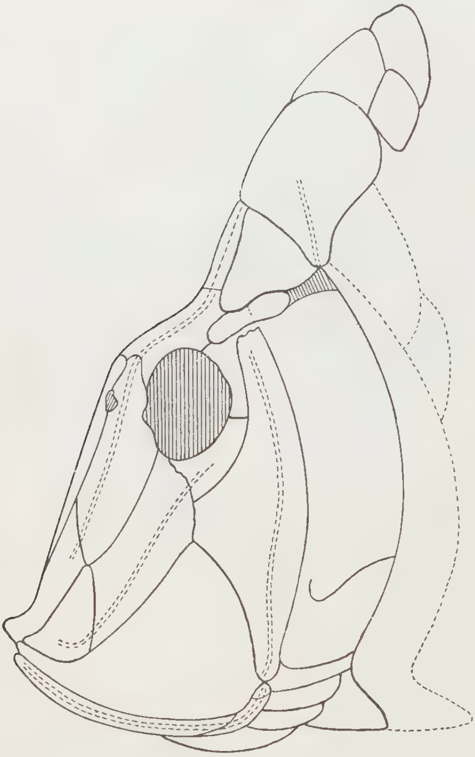


Fig. 90. *Platysomus parvulus* Williamson. Skull seen from the left side. After GREGORY (1933), fig. 15 B on p. 117.

my fig. 43), *Lactophrys tricornis* (L.) (fig. 166) (see my fig. 118) and *Periophthalmus* (fig. 228) (see my fig. 41). Finally, the great height of the new upper jaw is due to the maxillare only in *Polypterus* (fig. 10), † *Cheirolepis trailli* Agassiz (figs 12 A, 283 A, 286 A) (see my fig. 95), † *Palaeoniscus macropomus* Agassiz (fig. 12 B), † *Coccocephalus wildi* Watson (figs 12 C, 283 B, 286 B), † *Perleidus woodwardi* Stensiö (figs 21 A, 283 C, 286 C), *Scopelarchus anale* (Brauer) (fig. 90) and *Lates niloticus* (Gmel.) (figs 114, 298) (see my fig. 115).

By the side of these vertically high new upper jaws, low upper jaws are also found. GREGORY (1933) mentions for some genera that the upper jaw is thin, the consequence of which is that it will be low in a vertical direction. This is the case in *Gastrostomus*, where the maxilla is rod-like (p. 212, fig. 94) (see my fig. 87), and in *Cyclothone* where the jaws are slender bars (p. 159, fig. 54).

Of new upper jaws, low in the vertical direction, a number of examples may be derived from the illustrations given by GREGORY (1933). We mention: *Acipenser sturio* L. (fig. 20) (see my fig. 74), *Dorosoma erebi* (Gthr) (*Chatoëssus erebi*) (fig. 39) (see my fig. 29), *Engraulis encrasicholus* (L.) (fig. 40) (see my fig. 76), *Coila nasus* Temm. Schl. (fig. 41) (see my fig. 77), *Opisthoproctus* (fig. 43) (see my fig. 84), *Gonostoma elongatum* Gthr (fig. 53), *Chauliodus sloanei* Bl. Schn. (fig. 55) (see my fig. 122), *Stomias boa* Risso (fig. 56), *Osteoglossum* (fig. 57) (see my fig. 116), *Heterotis niloticus* (Cuv.) (fig. 58), *Eurypholis boissieri* Pictet (fig. 83), *Synodus foetens* (L.) (fig. 86), *Saurus myops* (Bl. Schn.) (fig. 87), *Tylosurus marinus* Walbaum (figs 99, 289 A, 291 E) (see my fig. 94), *Chiasmodon* (fig. 137), *Echeneis* (fig. 199), *Melanocetus* (fig. 272), *Lophodolos* (figs 274, 276 A) and *Lasiognathus* (figs 275, 276 B).

After this discussion of the upper jaw, that of the relative size of the snout of the higher Pisces may follow. Here, too, most data will be derived from GREGORY (1933), and I want to remind the reader that, what is called snout here, is sometimes called snout, but also rostrum, preorbital part of the skull, proboscis, muzzle *etc.* by GREGORY.

As we formulated above, we shall, in this article, understand by snout the preorbital part of the skull up to the front point of the new upper jaw, so the region between the orbiton (*i.e.* the most anterior point of the orbita) and the praemaxillon or the praemaxillare tip (*i.e.* the most anterior point of the praemaxillare in the norma lateralis); terms which are used by Gregory (1933, p. 420). Now, this praemaxillon may coincide with the prosthion (p. 420) in the sense of the most anterior point of the entire preorbital part of the skull, when there is *viz.* no secondary rostrum which juts out in front of the new upper jaw. This coincidence is, however, not necessary and does not occur when there is a secondary rostrum. If, however, these two anterior points do coincide, then the length of the snout in our sense, coincides with Gregory's effective rostral length which he defines as the distance from the prosthion to the projection of the orbiton on the horizontal (*i.e.* the line joining the prosthion and the pygidion; pygidion being the mid-point of the narrowest part of the caudal peduncle) (p. 420).

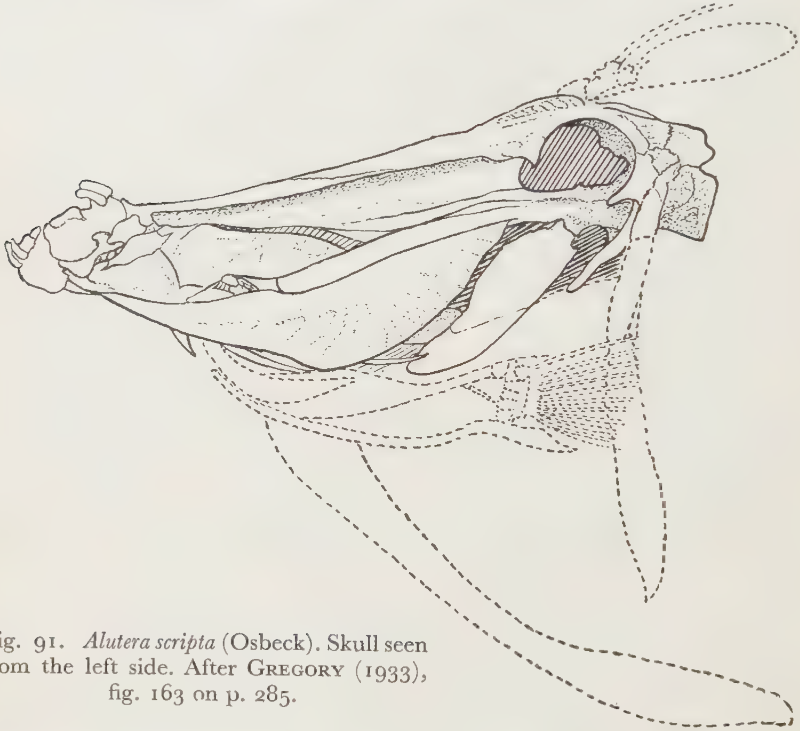


Fig. 91. *Alutera scripta* (Osbeck). Skull seen from the left side. After Gregory (1933), fig. 163 on p. 285.

Let us first discuss the relative measurement of the snout according to the longitudinal axis. Gregory (1933, p. 444) says about this that the ratio of the preorbital length to the head length varies only within relatively narrow limits in adults of a given species.

As regards the general connection between the length of the snout and the general shape of the skull in Teleostei, a long snout may, according to Gregory (1933, p. 431), occur among the species with a vertically deepened occiput, so, with the high skulls such as *e.g.* in *Alutera* (figs 163, 165, 290 C) (see my fig. 91), and among the skulls with a low occiput, so the low skulls, such as *e g.* in *Tylosurus* (figs 99, 289 A, 291 E) (see my fig. 94), while with the wide, low heads with a broad neurocranium we find a short snout, such as *e.g.* in *Myoxocephalus* (figs 213 B, 215 A, 299) (see my figs 22 and 92).

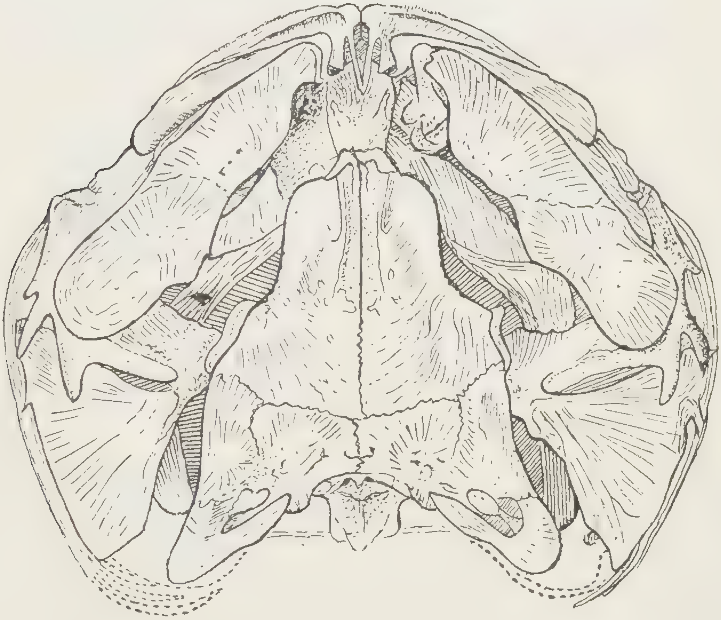


Fig. 92. *Myoxocephalus jack* (C. V.). Skull seen from above. After Gregory (1933), fig. 213 B on p. 334.

Between the length of the snout and the length of the jaws, also that of the new upper jaw, there is no direct connection. As Gregory (1933, p. 453) expresses it: there is the greatest diversity in the association of jaw length and snout length. And, although in the illustration to which Gregory refers (fig. 301) the outline of the animal is drawn with its soft parts, and not that of the skeletal snout and of the skeletal new upper jaw, yet the main types remain the same (see also pp. 302, 418). These main types are the following:

1. the snout is long and the upper jaw is short, because it is situated at the end of a long preorbital part of the skull; this main type occurs in a very pronounced way in *Aulorhynchus* (fig. 301 B) and in *Fistularia* (figs 105, 289 B) (see my fig. 93) and related species;

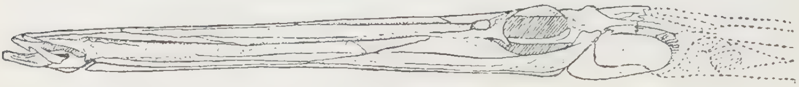


Fig. 93. *a. Fistularia* sp. Skull seen from the left side. After Gregory (1933), fig. 105 on p. 226.

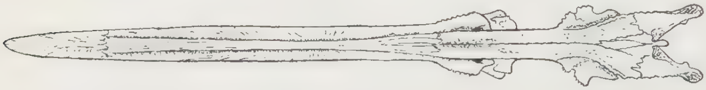


Fig. 93. *b. Fistularia* sp. Skull seen from above. After Gregory (1933), fig. 294 C on p. 430.

2. the snout is long and the upper jaw is long, this main type occurs in a very pronounced way in *Tylosurus* (figs 301 A, also 99, 289 A, 291 E) (see my fig. 94);

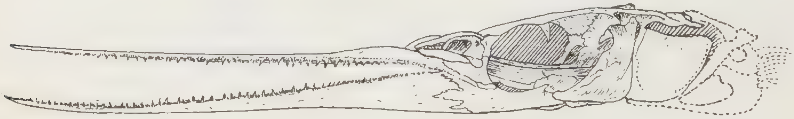


Fig. 94. *Tylosurus marinus* (Walbaum). Skull seen from the left side. After Gregory (1933), fig. 99 A on p. 221.

3. the snout is short and the upper jaw is long, so the slit of the mouth continues till far behind the eye; this is clearly the case in *Lampanyctus* (fig. 301 C), in *Gastrostomus* (p. 213, fig. 94) (see my fig. 87) and in † *Cheirolepis* (figs 12 A, 283 A, 286 A) (see my fig. 95) where, consequently, a good part of the jaws lies behind the orbiton (p. 421);

4. the snout is short and the upper jaw is short, so the slit of the

mouth does not continue far behind the eye; this main type occurs in *Copelandellus* (fig. 301 D).

The main type first mentioned, which occurs in a number of higher Pisces, is, for Vertebrata in general a very exceptional condition.

Among the Thoracostei we find a clear elongation of the preorbital part of the face in *Gasterosteus trachurus* C. & V., in *Gasterosteus spinachia* L. this elongation is decidedly longer and it is carried to an extreme in *Aulostomus* and still more so in *Fistularia* (see my fig. 93), of which it is said that it has an excessive elongation of the preorbital face and an amazingly great prolongation of the region between the eyes and the mouth, and of which, consequently, the ethmo-vomer block is greatly elongated; in the Syngnathidae, such as in *Phyllopteryx foliatus* (Shaw) the skull is fundamentally the same as in *Fistularia* (see my fig. 93), but even more specialized; *Centriscus*, finally, shows, with regard to *Gasterosteus spinachia* L. a marked elongation of the snout (pp. 224, 225, 226, 417, 438; text of fig. 294; figs 102–109). These forms show what Böker (1937, pp. 54/55) calls a "Röhrenmaul" (tubulous mouth cavity). – Certain Mormyroidea, such as *Gnathonemus curvirostris* Blgr., show a long, decurved, tube-like prolongation of the preorbital part of the face, whereas the related *Petrocephalus* has undergone a rapid shortening of this proboscis or bony tract, which has brought the mouth beneath the orbita instead of far in front of it (pp. 171–173, 417, figs 63, 64) (see my figs 66 and 88). – In *Rhamphichthys rostratus* (L.) the snout is very long, the

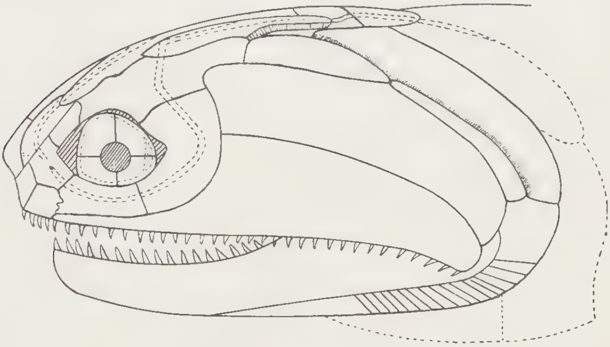


Fig. 95. *Cheirolepis traill* Agassiz. Skull seen from the left side. After Gregory (1933), fig. 12 A on p. 113.

mouth very small, the whole recalling somewhat the form of the snout in certain Mormyridae (p. 189). – In certain Chaetodontoidei the ethmoidal region is lengthened by prolongation of the lacrimal and ethmoidal skeletal elements; this is found in *Platax*, *Chaetodipterus* and especially in *Angelichthys* and *Pomacanthus* with a clear protrusion of the preorbital face (pp. 282, 422, see also p. 277; figs 151, 152, 153, 154, 290 A) (see my fig. 126). Even in *Pomacanthus*, however, the type of a small mouth at the end of a long snout is hardly reached, but this condition must be regarded as a line of development in the direction of the Balistoidei. – Among the Balistoidei we find in *Zanclus*, in opposition to the Chaetodontoidei mentioned, that this forward growth of the ethmoid region is emphasized to a hitherto unheard-of degree (p. 282, fig. 158) (see my fig. 117). GREGORY (1933, fig. 165, see also figs 159–163, 290) (see my figs 43 and 91) reproduces the snout or protrusion of the preorbital face with the upper jaw situated at the end of it, according to the increase in length in *Teuthis*, *Triacanthus*, *Balistes*, *Alutera* and *Anacanthus*; this last-mentioned genus carries the grotesque specialization of *Alutera* to an amazing extreme (p. 286). In these Balistoidei the ethmovomer block shows a forward growth (p. 438). In the Ostraciontidae as in *Lactophrys*, which resembles *Triacanthus* in its elongate face, the snout is prolonged (p. 289, fig. 166) (see my fig. 118), but in *Spheroides* we find already a marked relative shortening of the face (p. 289, fig. 167) and, according to a hypothesis of GREGORY'S (pp. 288/289) the whole plectognath stock shows a marked secondary shortening of the snout. Accordingly, in *Lagocephalus* we find a marked shortening of the preorbital face length (pp. 290, 292, fig. 168), and in Diodontidae the secondary shortening of the snout goes very far (p. 293, fig. 170) (see my fig. 121) so that here there is no question of a snout with a new upper jaw situated at the end of it. Whether this is also the case in *Gomphosus*, which according to GREGORY (1933, p. 257) has the face elongated anteroposteriorly into a tubiform snout, cannot be decided without a picture.

Examples of the second main type (long snout, long upper jaw) besides *Tylosurus* (see my fig. 94) which we already mentioned, are the following. *Istiophorus* shows a great development of the snout from the praemaxillaria and maxillaria (p. 316, fig. 196); *Lepisosteus* shows a great elongation of the snout (p. 127, figs 24, 287 D) (see my fig. 65); in *Sphyraena barracuda* (Walbaum) a forward growth of the jaws is combined with a lengthening of the lacrimal and ethmoid region (pp. 266/267, fig. 141), *Trichiurus* possesses a forward growth of both snout and jaws (p. 302, figs 195, 291 D). Among the Labridae with a forward elongation of the snout, we may call snout and upper jaw very long in *Tautogolabrus adspersus* (Walbaum), whereas they are less long in *Lachnolaimus maximus* (Walbaum) (p. 256, figs 129, 130) (see my figs 81 and 129). In *Haemulon* the snout in front of the lacrimale is long, the upper jaw is long as well (p. 248, fig. 121) (see my fig. 127). Relatively elongate are both snout and upper jaw, which have grown forward, in † *Furo* (*Eugnathus*) (pp. 131, 132, fig. 27) and, in my opinion also in *Albula* with its elongation and marked increase of the length of the snout (p. 144, fig. 37) (see my fig. 125), and in *Anableps tetrophthalmus* Bl. where the jaws lie wholly in front of the orbitae (p. 220, fig. 98) (see my fig. 40). From the pictures given we still point out that of *Esox masquinongy* Mitchill (fig. 95) (see my fig. 30), *Belonesox belizanus* Kner (fig. 96 B), *Rhachycentron* (fig. 186) (see my fig. 120), *Echeneis* (fig. 199), *Prionotus evolans* (L.) (fig. 218), *Trigla hirundo* Bl. (fig. 219), *Mastacembelus* (fig. 233) and *Parachaenichthys georgianus* (Fischer) (fig. 239 C).

The third main type comprised the skulls with a short snout and long jaws, of which we mentioned *Lampanyctus*, *Gastrostomus* and † *Cheirolepis* as examples (see my figs 87 and 95). Further examples are † *Hoplopteryx lewesiensis* (Mantell) with its short snout, but long upper jaw (p. 233, fig. 110), *Antennarius* and allied Pediculati which show a shortening of the preorbital region, while the upper jaw is long (pp. 390/391, fig. 265), and *Tarpon atlanticus* (C. & V.) with its relative shortness of the snout combined with a long upper jaw (p. 138, fig. 31) (see my fig. 85). Of the pictures given we still mention *Polypterus* (fig. 10), † *Palaeoniscus macropomus* Agassiz (fig. 12 B), † *Coccocephalus wildi* Watson (figs 12 C , 283 B, 286 B), † *Perleidus woodwardi* Stensiö (fig. 21 A, 286 C), *Amia calva* L. (fig. 28), † *Pholidophorus macrocephalus* Agassiz (fig. 29), *Salmo* (fig. 45), *Gonostoma elongatum* Gthr (fig. 53), *Chauliodus sloanei* Bl. Schn. (fig. 55) (see my fig. 122), *Stomias boa* (Risso) (fig. 56), *Osteoglossum* (fig. 57) (see my fig. 116), *Notopterus* (fig. 61), *Erythrinus unitaeniatus* Spix (fig. 67) (see my fig. 28), *Lycodontis funebris* (Ranzani) (fig. 82 B) (see my fig. 119), *Synodus foetens* (L.) (fig. 86), *Saurus myops* (Bl. Schn.) (fig. 87), *Omosudis lowii* Gthr (*Osmosudis lowii*) (fig. 89), *Scopelarchus* *anale* (Brauer) (fig. 90), *Evermanella atrata* (Alcock) (fig. 91), *Cetomimus regani* Zugmayer (fig. 92), *Myctophum humboldti* (Risso) (fig. 93), *Lates niloticus* (Gmel.) (figs 114, 298) (see my fig. 115), *Chiasmodon* (fig. 137), *Polydactylus* (fig. 144), *Ophicephalus* (fig. 145), *Aspicottus* (*Enophrys*) (fig. 216), *Symbranchus marmoratus* Bl. (fig. 231) (see my fig. 123), *Trachinus* (fig. 243), *Zoarces anguillaris* (Peck) (fig. 253), *Fierasfer* (fig. 257) and *Opsanus tau* (L.) (fig. 263). In this connection we also mentioned *Salmo*, on the ground of the picture in Gregory. We point out, however, that, according to Holmgren & Stensiö (1936, p. 486) the ethmoidal regionin *Salmo* takes up more than one third of the length of the skull, which, in my opinion must be accompanied by a great length of the snout.

Under the fourth main type (snout and upper jaw both short), we may bring, besides the example already given (*Copelandellus*): *Iniistius*, where the jaws are short anteroposteriorly, and the snout is short, too (p. 257, fig. 132) (see my fig. 128), the Gobioidei with their short snout, such as *e.g. Periophthalmus* (p. 346, fig. 228) (see my fig. 41) and also † *Portheus molossus* Cope with its short snout, but already relatively long new upper jaw (p. 144, figs 36, 288 B). *Alabes*, which, contrary to *Monopterus*, has an extreme shortening of the telescoping snout, has, in all probability, a short upper jaw, too (p. 352, fig. 232). In *Pelor japonicum* C. V. the ethmo-vomer block is greatly shortened, while also the upper jaw is relatively short (p. 438, fig. 206) (see my fig. 124). Of the pictures given by Gregory we want to point out that of *Eigenmannia macrops* (Blgr.) (fig. 73 A) (see my fig. 80).

As regards the measurements of the snout in the transverse direction in higher Pisces, Gregory gives the following information. In the broad and short type of skull among Teleostei mentioned above, the snout is probably broad, as well (p. 431). *Lactophrys* has a narrow snout (p. 289) as has also *Stylophorus chordatus* Shaw (p. 300). Whereas in *Scomber* the skull is narrow in front, *Scomberomorus* shows a broadening of the prefrontal area, and the Thunnidae are broad-snouted and show a great breadth across the ethmoid region and great massiveness (pp. 310, 311, 315, figs 189, 191, 192). *Mugil cephalus* L. shows a thickening of the snout and the skull is relatively very wide in front (p. 268, fig. 143), in *Cottus octodecimspinosus* (Mitchill) (*Myoxocephalus octodecimspinosus*) the skull as a whole is notably broader than that of *Sebastes*, but in *Myoxocephalus jaok* (C. V.) and allied species, the breadth becomes extreme; from the picture it appears that the front part of the skull is broad, too (p. 333, fig. 213 B) (see my fig. 92); in *Pelor japonicum* C. V. the ethmo-vomer block is greatly widened (p. 438, fig. 206). According to the pictures given by GREGORY the snout is also broad in *Polypterus* (fig. 11), *Amia calva* L. (fig. 23 B), *Tarpon atlanticus* (C. & V.) (fig. 33), *Erythrinus unitaeniatus* Spix (fig. 68), *Electrophorus electricus* (L.) (fig. 72 B), *Labeo* (fig. 75 A), *Hydrocyon* (fig. 75 B), *Heterobranchus longifilis* C. & V. (fig. 77 A), *Chrysichthys* sp. (fig. 77 B), *Orestias* (fig. 97 A), *Lates niloticus* (Gmel.) (figs 115, 118, 293 A) (see my fig. 21), *Ophicephalus* (fig. 146 A), *Anabas* (fig. 146 B), *Diodon hystrix* L. (fig. 171), *Rachycentron* (fig. 187), *Echeneis* (fig. 198), *Scorpaena scrofa* L. (fig. 203 B, see also fig. 213 A), *Platycephalus* (fig. 211), *Cyclopterus* (fig. 217), *Trigla hirundo* Bl. (fig. 221 A), *Dactylopterus* (fig. 223 B), *Eleotris pisonis* (Gmel.) (fig. 229 A), *Periophthalmus* (fig. 229 C), *Cottoperca gobio* (Gthr) (fig. 241 A), *Notothenia macrocephala* Blkr (fig. 241 B), *Dactylagnus* (fig. 244), *Crapatalus* (fig. 244), *Uranoscopus* (fig. 244), *Trachinus* (fig. 245 A), *Kathetostoma* (fig. 245 B), *Astroscopus* (fig. 248) (see my fig. 148), *Gobiesox* (fig. 250), *Zoarces* (fig. 254 B), *Anarhichas* (fig. 254 C), *Lota* (fig. 259 A), *Opsanus* (fig. 263 B), *Lophius piscatorius* L. (fig. 267 B), *Lophodolos* (fig. 276 A) and *Pomatomus* (fig. 294 A).

According to the pictures in GREGORY the snout is narrow in *Lepisosteus tristoechus* (Bl. Schn.) (fig. 23 A) (see my fig. 51), *Albula vulpes* (L.) (fig. 37 D), *Alepocephalus rostratus* Risso (fig. 51), *Eigenmannia macrops* (Blgr.) (fig. 72 A), *Carpiodes* (fig. 76 B), *Aulopus* (fig. 85), *Esox masquinongy* Mitchill (fig. 95 B), *Dallia* (fig. 95 C), *Fundulus* (fig. 97 B), *Belonesox* (fig. 97 C), *Sphyraena barracuda* (Walbaum) (fig. 142), *Atherinopsis californiensis* Girard (fig. 143 B), *Promethichthys prometheus* (C. V.) (fig. 194 A), *Hexagrammos* (fig. 209 B), *Symbranchus* (fig. 231), *Ammodytes* (fig. 234), *Parachaenichthys* (fig. 241 C), *Callionymus* (fig. 242), *Gadus* (fig. 259 B) and *Lasiognathus* (fig. 276 B). – According to the pictures in GREGORY the snout is very narrow in *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*) (fig. 65), *Tylosurus acus* (Risso) (fig. 100), *Luciolates* sp. (fig. 117), *Sphyraena argentea* Girard (fig. 143 A), *Lepidopus caudatus* (Euphrasen) (fig. 194 B), *Centropomus* (fig. 294 B) and *Fistularia* (fig. 294 C) (see my fig. 93).

The following data in GREGORY probably refer to the vertical diameter, so to the height of the snout. In *Esox masquinongy* Mitchill the snout is stretched laterally into a thin, flattened surface (p. 216, fig. 95 A) (see my fig. 30), in *Microspathodon* the snout shows a downward prolongation (p. 255, fig. 128). The information that *Zoarces anguillaris* (Peck) shows a relatively heavy muzzle, perhaps refers to the vertical diameter of the snout as well (p. 375, fig. 254). The information that *Lates niloticus* (Gmel.) has a sharp snout (p. 242) must refer to the height (see my figs 21 and 115).

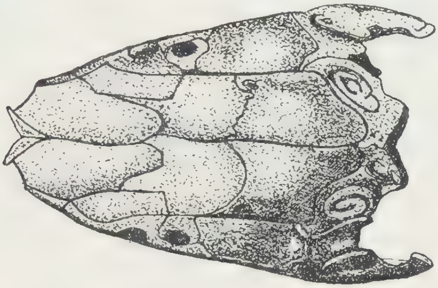
From the pictures in GREGORY (1933) we can deduce that the snout is low in *Lepisosteus tristoechus* (Bl. Schn.) (figs 24, 287 D), *Gnathonemus curvirostris* Blgr. (fig. 63) (see my fig. 66), *Tylosurus* (figs 99, 289 A, 291 E) (see my fig. 94), *Fistularia* (figs 105, 289 B) (see my fig. 93), *Phyllopteryx foliatus* (Shaw) (fig. 106), *Centriscus* (*Amphisile*) (figs 108, 109), *Echeneis* (fig. 199) and *Parachaenichthys georgianus* (Fischer) (fig. 239 C). Relatively low is the snout in *Sphyraena barracuda* (Walbaum) (fig. 141, see also fig. 284), *Gadus* (fig. 258 A) and *Lota* (fig. 258 B). A short snout is very soon high too, as many pictures show.

In † Stegocephala, as we already saw in the discussion of the absolute size, the elements of the new upper jaw are more important and larger than in Teleostomi (VERSLUYS, 1936, p. 717). Consequently the new upper jaw is, also relatively, larger with regard to the skull, the head and the entire body.

In recent Amphibia the new upper jaw is relatively very long, which is connected with their way of taking food. The new upper jaw is well developed in width, too. It is however, weakly developed, in the sense that it is very low, which is connected with the fact that it plays only a slight part in the mastering and the consumption of the food.

Owing to the broad rostral rounding of the new upper jaw and the far rostral situation of the orbitae, the snout of recent Amphibia is short and broad. In the grubbing Caecilia, however, the head has become wedge-shaped (BÖKER, 1935, p. 167) (see my fig. 96), which, for the greater part, is due to the shape of the snout. In a number of genera of the Hylinae a broad, spatulate, strongly protruding snout has developed (STADTMÜLLER, 1936, pp. 600/601) (see my fig. 97).

In Amniota the connection between the relative size of the new upper jaw with regard to the skull, the head or the entire body, is much better known, as well as the part played by the upper jaw in the taking of the food, in the second place in mastering the food (in both cases showing a connection with the kind of food), and in the third place in certain accessory functions (the use of the teeth as a weapon, of jaw and teeth in sexual play, of the teeth in biting through roots while grubbing, of dentition and jaw as prehensile organs, in locomotion, *etc.*) such as we indicated already above. This greater knowledge is connected with the greater knowledge of the higher classes of the Vertebrata in general, but also with the more important part the jaws play in the mastering of the food, and all sorts of accessory functions. The more important part played by the upper jaw of Amniota in the mastering of the food, leads to types of jaw which are clearly differently constructed from those, serving only or principally for the seizing of food. In this connection we point with Marinelli (1933, p. 202) to the essential difference in size and shape of the jaws and their situation (with regard to the cerebral skull)



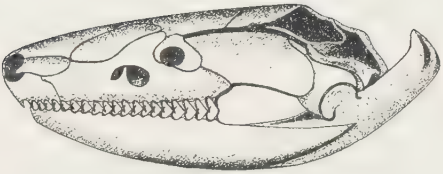


Fig. 96. *a. Ichthyophis glutinosus* (L.). Skull seen from above. 4.5×. After P. & F. Sarasin (1890), pl. XV, fig. 1.

Fig. 96. *b. Ichthyophis glutinosus* (L.). Skull seen from the right side inverted. 4.5×. After P. & F. Sarasin (1890), pl. XV, fig. 3.

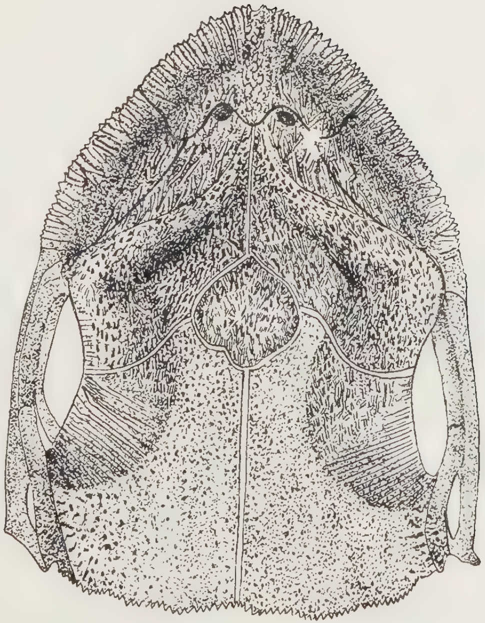


Fig. 97. *a. Triprion petasatus* (Cope).
Skull seen from above. R.M.N.H. Leiden, no. 9161*a*. 4.5×.
Original drawing by G. W. M. Kurpershoek.

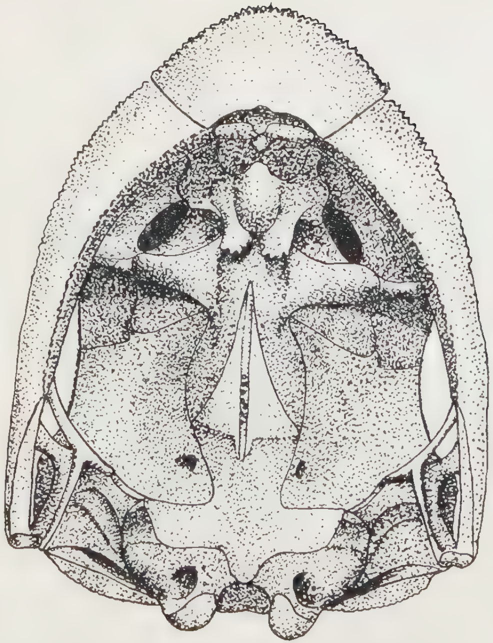


Fig. 97. *b. Triprion petasatus* (Cope).
Skull seen from below. R.M.N.H. Leiden, no. 9161*a*. 4.5×.
Original drawing by G. W. M. Kurpershoek.

in animals which snap up their prey ("Schnapper") where the construction of the apparatus of the jaws aims at swiftness of motion ("mit vorwiegender Geschwindigkeitsleistung") and in biting animals ("Beisser") where vigour of the jaws is specially aimed at ("mit vorwiegender Kraftleistung"). In Aves the principal function of the bill is that of prehensile organ (see my fig. 98), and not that of an organ whose task it is to cut up the food or prepare it in any other way. This latter is a very striking function of the jaw of Mammalia (see my fig. 99). Owing to this fact, the development of the jaw in Aves and Mammalia is so entirely different, and this explains why Aves and Mammalia, though they have the great development of the brain in common, and though both classes can be derived from Reptilia, have such different skulls (MARINELLI, 1936, p. 809).

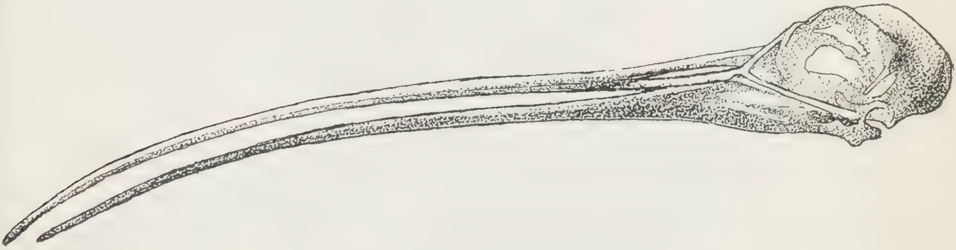


Fig. 98. *a. Numenius arquata* (L.). Skull seen from the left side. R.M.N.H. Leiden, no. 9457. 0.6×. Original drawing by J. F. OBBES.

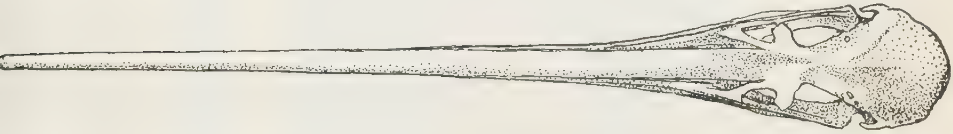


Fig. 98. *b. Numenius arquata* (L.). Skull seen from above. R.M.N.H. Leiden, no. 9457. 0.6×. Original drawing by J. F. OBBES.

In Reptilia there is clearly a close connection between length and breadth of the new upper jaw and the character of the food, which is mainly connected with the way of seizing the food, and partly also the way in which the food is prepared by the jaws.

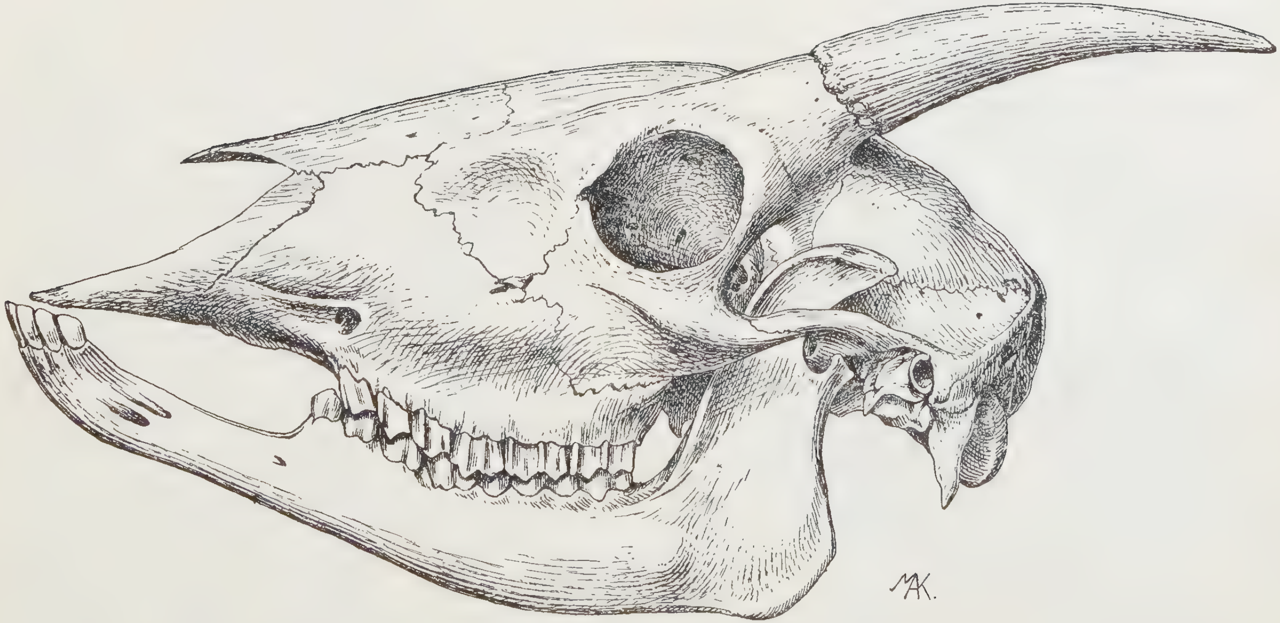


Fig. 99. *a. Capricornis sumatraensis* (Bechstein) ♂. Skull seen from the left side. R.M.N.H. Leiden, no. 991/'20. 0.47×. Original drawing by M. A. Koekkoek.

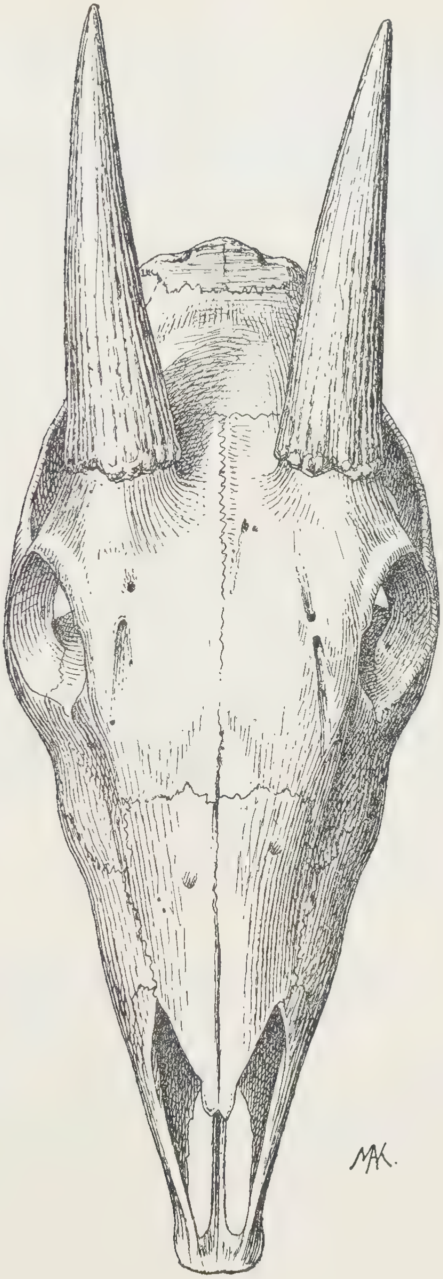


Fig. 99. *b. Capricornis sumatraensis* (Bechstein) ♂. Skull seen from above. R.M.N.H. Leiden, no. 991/'20. 0.47×. Original drawing by M. A. Koekkoek.

This connection between the lengthening of the jaws and the snout on the one hand and the character of the food on the other, is very clear among Loricata (Owen, 1866 I, p. 159; Williston, 1925, pp. 287, 290; Versluys, 1936, pp. 706, 718, 789; Böker, 1937, pp. 24, 62). A very slender snout is found in ancient † Teleosauria and recent Gavialidae, where the jaws have been lengthened out of all proportion, and are, moreover, bill-like in their narrowness; Gavialidae seize their prey, fish, rapidly and swallow it rapidly (see my figs 54, 100). In the genus *Crocodylus* the snout is less elongate; they are beasts of prey (see my fig. 101). There are also Loricata (Crocodilia) with rather short and broad, blunt snouts, with which they can firmly hold their prey; this condition is found in omnivorous genera like *Osteolaemus*, *Alligator* and "Caiman" (see my fig. 102). In the sub-division of the Crocodylidae the snout is, consequently, never slender. In Loricata the strongly elongated jaws and snout wherein there is room for many teeth, serve to hold the large prey; this is combined with a very firm structure of the skull and at the same time akinesis (Böker, 1937, p. 62). – Many forms with – in proportion to the rest of the skull – long, sometimes very long, but often pointed

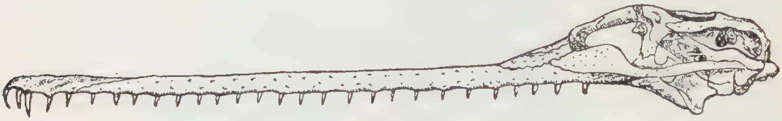


Fig. 100. *a. Tomistoma schlegelii* (S. Müller) (*Gavialis gangeticus* (Gmelin)). Skull seen from the left side. 0.52×. After C. B. Brühl (1862), Tab. X, fig. 1.

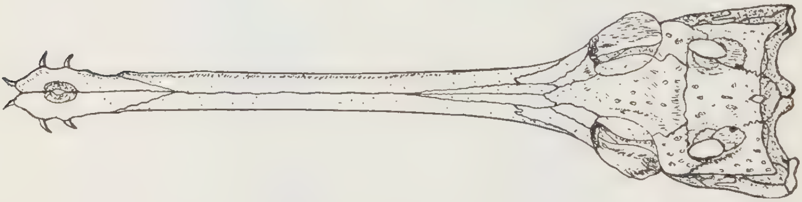


Fig. 100. *b. Tomistoma schlegelii* (S. Müller). Skull seen from above. 0.52×. After C. B. Brühl (1862), Tab. VIII, fig. 3.

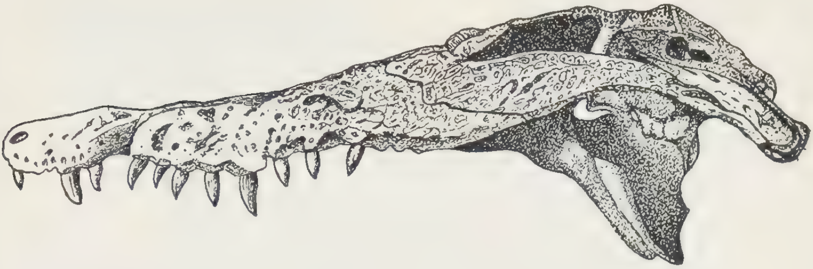


Fig. 101. *a. Crocodylus vulgaris* (Cuv.). Skull seen from the left side. 0.27×. After J. Versluys, in Bolk, Göppert, Kallius and Lubosch (1936), IV, fig. 611 on p. 792.

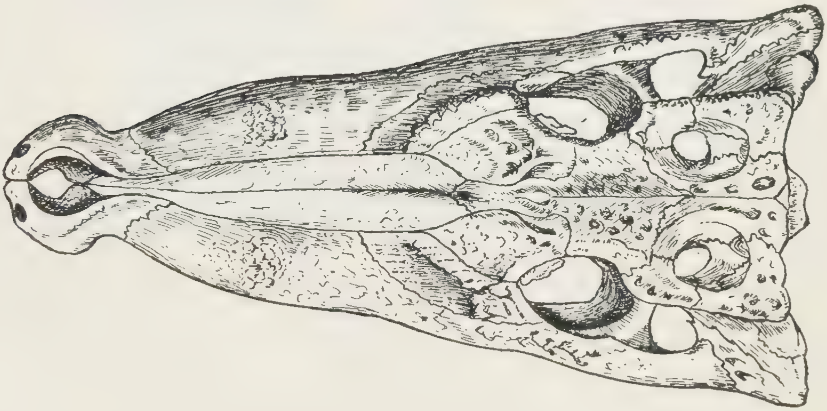


Fig. 101. *b. Crocodylus vulgaris* (Cuv.). Skull seen from above. 0.22×. After K. Patterson Schmidt (1919), fig. 4 on p. 423.

and hardly high or hardly broad snouts are found not only among the Loricata, but also among other aquatic Reptilia, such as † Phytosauria, † Champsosauridae, † Mesosauria, † Thalattosauria and † Ichthyosauria (Owen, 1866 I, p. 159; Williston, 1925, pp. 9, 79, 253, 255, 290; Versluys, 1936, pp. 706, 788, 797, 798) (see my figs 53 and 103).

Among terrestrial Reptilia we find also a clear connection between the length of the new upper jaw and the snout and

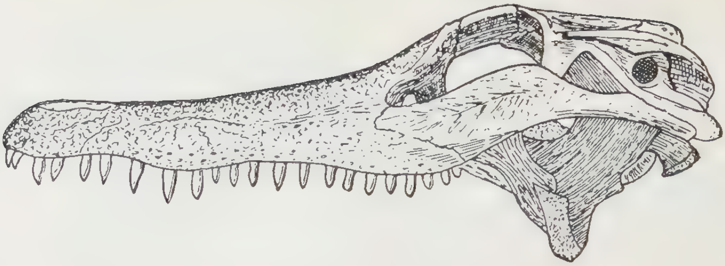


Fig. 102. *a. Alligator.* Skull seen from the left side. 0.5×. After Williston (1925), fig. 69 c on p. 85, completed after nature.

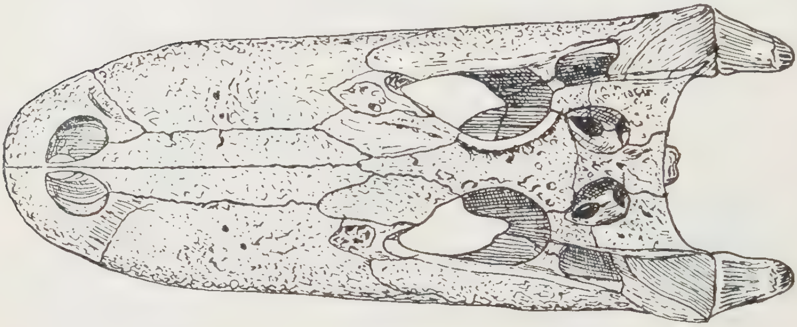


Fig. 102. *b. Alligator.* Skull seen from above. 0.5×. After Williston (1925), fig. 69 a on p. 85.

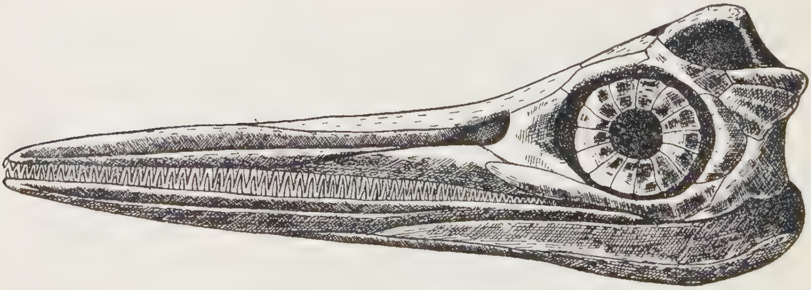
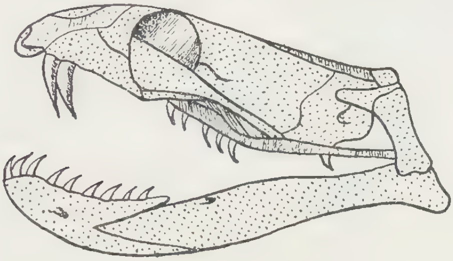


Fig. 103. *Stenopterygius acutirostris* (Owen). Skull seen from the left side. 0.08×. After Abel (1919), fig. 354 on p. 455.

the character of the food, especially connected with the way of seizing it.

In those species which catch worms and insects, but also in beasts of prey with larger prey, we find a long and narrow snout (Versluys, 1936, p. 706). Such long and narrow jaws are yet relatively voluminous by reason of their great length. The long and narrow upper jaw of a mouth that can be widely opened is extremely well-suited to the rapid and sure seizing of the last mentioned prey, while, at the same time the kinesis fits it (Williston, 1925, p. 9; Versluys, 1936, pp. 719, 741, 742). The solution is different in Chamaeleontidae, they catch the insect prey with their tongue, and, consequently, the snout is short (Versluys, 1936, p. 779) (see my fig. 32).



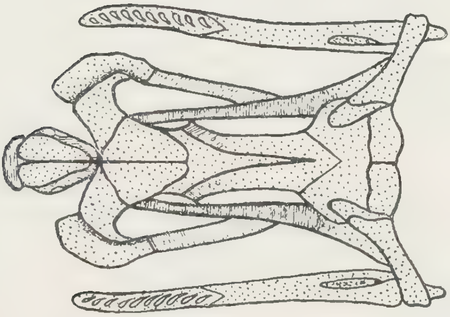
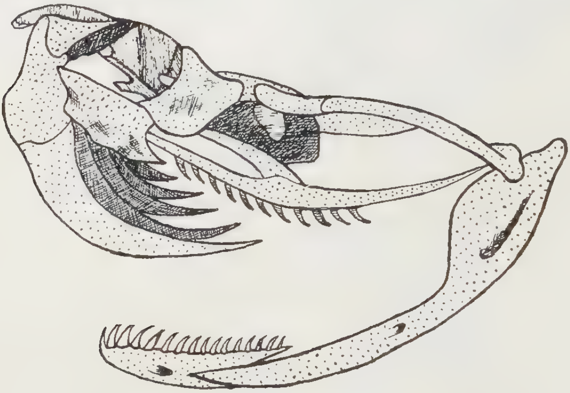


Fig. 104. *a. Micrurus corallinus* (Wied). Skull seen from the right side inverted. After M. Phisalix (1912), fig. 30.

Fig. 104. *b. Micrurus corallinus* (Wied). Skull seen from above. After M. Phisalix (1912), fig. 30.

Among the Serpentes (Ophidia) the length of the new upper jaw differs greatly. Within the Serpentes (Ophidia) Böker (1937,

p. 123) distinguishes the following two types: in the first type the upper jaw has been strongly shortened; this occurs in proteroglyphous Serpentes (Ophidia) such as *Micrurus* (*Elaps*) (see my fig. 104), *Naja* and also in Hydrophiidae; in the second type the upper jaw is so short that there is practically only room for one



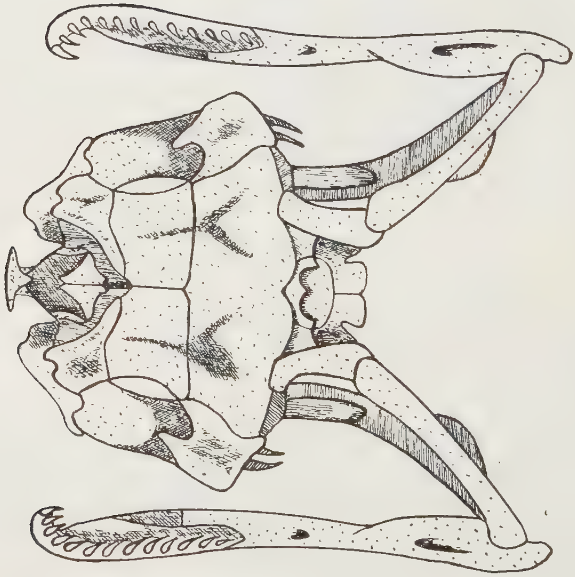


Fig. 105. a. *Bitis gabonica* (Dum., Bibr. & Dum.). Skull seen from the right side inverted. After M. Phisalix (1912), fig. 38.

Fig. 105. b. *Bitis gabonica* (Dum., Bibr. & Dum.). Skull seen from above. After M. Phisalix (1912), fig. 38.

tooth; to this second type belong the solenoglyphous Serpentes (Ophidia) such as *Vipera berus* (L.), *Bitis* (see my fig. 105), *Aspis* (*Cerastes*), *Lachesis* and *Crotalus*. In many Serpentes (Ophidia) the upper jaw is strongly kinetic, connected with the grasping of the prey and shifting it in the mouth cavity.

So, while kinesis offers an advantage in catching worms, insects and other small prey, akinesis offers an advantage in holding large prey, also among terrestrial Reptilia (VERSLUYS, 1936, pp. 789/790; BÖKER, 1937, p. 62). Reptilia that catch, grasp and firmly hold a prey which struggles vehemently possess jaws that are not too long (VERSLUYS, 1936, pp. 718, 719). In these Reptilia, with a struggling prey, but also in herbivores and durophages, the jaws are indeed short, but they are at the same time broad so that they are voluminous as well (WILLISTON, 1925, p. 9; VERSLUYS, 1936, pp. 705/706, 717).

In Reptilia jaws and snout are only slightly influenced by the demands of the mastering and consumption of the food. Of the accessory demands that may be made on the new upper jaw we mention that of the grubbing Serpentes (Ophidia) and Amphisbaenidae. Here the head has become a digging wedge, which, in my opinion, is due mainly to the form of the snout (BÖKER, 1935, p. 167) (see my fig. 96).

In Aves we are confronted by the difficulty mentioned above (p. 169), that the relation between the horny upper bill and the skeletal new upper jaw is very seldom known. So in the following we cannot do more than give data about length, breadth, height *etc.* of the horn bill.

BÖKER (1937, p. 89) points out that in the anatomical series † *Euparkeria capensis* Broom (one of the † Pseudosuchia), † *Archaeornis siemensi* (Dames), *Columba livia* (L.) dom. the facial skull becomes progressively lighter, that is to say, the upper bill becomes progressively lower and narrower, whereby, in Aves, the shortened maxillare and the lengthened intermaxillare have been reduced to thin rods.

Furthermore, we remind the reader of MARINELLI's opinion (1936, p. 811), that the length of the bill generally conforms more to the size of the body than the size of the brain does. Just as for the absolute size it also holds good for the relative size that there are such a number of exceptions that we can hardly speak of such a connection. The functions of the bill differ too much, and the character of the food is too different, while also the places or the environment where the food is looked for and seized are too heterogeneous for us to be able to speak of such a connection. We mention only the difference in the length of the bill and the size of the bill between *e.g.* Limicolae, Accipitres, Psittaci, Nectariniidae *etc.* mutually, but also within each of these groups.

In Aves the main function of the bill is that of a pair of pincers or a prehensile organ, independent of the food. The rod-like construction of the bill is connected with this function as a pair of pincers. With such a pincer-like character of the bill, its length is the most important thing; breadth and height are generally slight, so that such a bill is, also relatively, small in volume. With such a function of the bill, kinesis may be regarded as an advantage.

In general the bill of Aves is narrow and low so that the volume is small, great length notwithstanding. The proportion between the breadth of the bill and its length is in *Dryobates maior* (L.) 1 : 1.5; in *Corvus corax* L. it is 1 : 2.5; and in *Ardea cinerea* L. it is 1 : 4 (BÖKER, 1937, p. 30). In Picidae the bill – upper and lower bill together – have the shape of a four-sided pyramid (BÖKER, 1937, p. 30); in *Haematopus ostralegus* L. the narrow bill has a rectangular cross section (*l.c.*, p. 25).

The primitive bill of Aves is short and pointed, as it occurs in Birds eating insects and berries (BÖKER, 1937, p. 62). In Certhiidae and *Lepidocolaptes* the bill is long, thin and curved, in most woodpecker-like Dendrocolaptidae the bill is shorter (BÖKER, 1937, pp. 29, 90). In Picidae the bill is relatively short (*l.c.*, p. 30). In those Aves which catch their insect prey in the air, such as Caprimulgidae (especially *Nyctibeus* and *Podargus*), Micropodidae, (= Cypselidae) and Hirundinidae, the slit of the mouth has been broadened at the cost of the length of the bill, in contrast to other insectivores (STRESEMANN, 1929, p. 464; BÖKER, 1937, pp. 96/97, 107). In those Aves which get the insects, larvae, worms *etc.* out of the earth or water, we often find relatively long to very long, cone-shaped bills, such as in *Tringa*, Ciconiidae *etc.* (BÖKER, 1937, pp. 62, 63). The bill of *Scolopax rusticola* L. is relatively very long (BÖKER, 1937, p. 94) (see my fig. 36). Very often this bill is straight, as in *Haematopus*, *Scolopax etc. etc.* (*l.c.*, pp. 25, 94). But in other cases the bill is curved, upwards as in *Arenaria interpres* (L.), *Recurvirostra avocetta* L. *etc.*; sideways such as in *Anarhynchus frontalis* (Quoy & Gaimard); downwards such as in *Plegadis*, *Upupa*, *Nu-*

menius, Icteridae, Charadriidae *etc.* (Böker, 1937, pp. 25, 63, 94). In many other cases it is only the point of the upper bill that is hooked, such as in Larinae, Tubinares and Phalacrocoracidae (Böker, 1937, pp. 64, 65) (see my figs 13 and 56). This curved shape and this hook at the end of the upper bill influence its length; whether they also influence the length of the skeletal new upper jaw, I do not know. The length of the bill is no exact measure for the depth of the place where the prey is seized, for the long, pincer-like bill is not the only possibility to get worms and insects out of the earth, other Aves reach the same end with shorter bills by trampling on the ground (Stresemann, 1929, pp. 441/442).

Above we mentioned also all sorts of groups eating fish as well as worms and insects. Among the fish-catchers we find also other shapes of the bill by the side of curved ones, and such with a hooked end of the upper bill. Thus *Balaeniceps* has a very broad, unwieldy bill (Böker, 1937, p. 63) and Pelecanidae have an exceptionally strongly elongated and therefore broadened bill (*l.c.*, p. 64) (see my fig. 106).

Accipitres and Striges have relatively very short bills, because in these birds of prey, as opposed to Aegypiinae, it is not the bill with the sharp hook, but the legs that have the most important task in catching and killing the prey (Stresemann, 1929, p. 465; Böker, 1937, p. 146).

In the herbivorous Aves the bill is always broad and powerful – consequently: high – and curved bills occur practically never, in contrast to Aves eating (animal) prey (Böker, 1937, p. 104). But differences in the structure of the bill, connected with the character of the food, are found in closely related species. Such differences are found among the Psittaci, in the genera *Ara*, *Amazona* and *Probosciger*, which, with their large bills crack very hard palm-nuts (Stresemann, 1934, p. 820). As an exceptional case we want to point out that in the bills of *Loxia curvirostra* L. the curve in the upper bill influences its length *etc.* (Böker, 1937, p. 26).

In a number of cases the mastering of the food, its consumption, and chopping up also belongs to the functions of the bill, apart from the seizing of it, even if those functions do not play the most important part. Where this function falls to the part of the bill, we see the necessary structure appear in the length, breadth and height of the upper bill. In this connection we again point to the

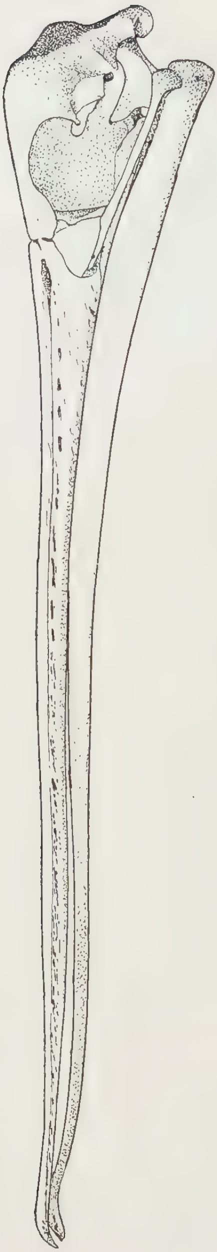


Fig. 106. *a. Pelecanus rufescens* Gm. Skull seen from the left side. R.M.N.H. Leiden, cat. b. 0.42×. Original drawing by J. F. Obbes.

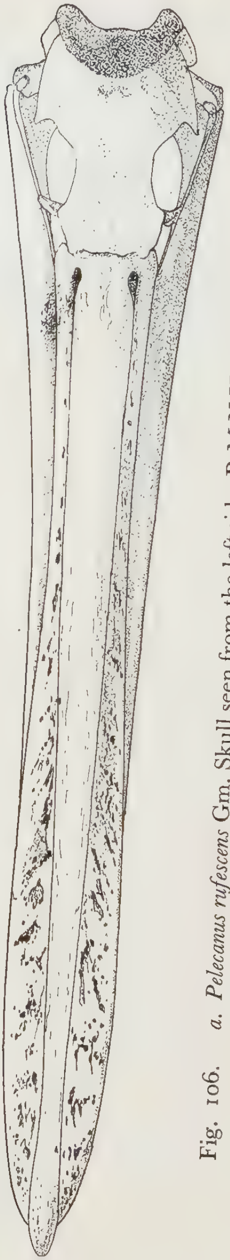


Fig. 106. *b. Pelecanus rufescens* Gm. Skull seen from above. R.M.N.H. Leiden, cat. b. 0.42×. Original drawing by J. F. Obbes.

example of Psittaci mentioned above, wherein the function of cracking palm-nuts, doubtlessly plays a part. In Passeres the bill is powerful, but it also serves in partially cutting up the seeds, which in Galli, Columbae and Anserinae entirely happens in the gizzard (Stresemann, 1929, p. 459). The bill of Accipitres has an important function in the cutting up of the prey, so that the particulars in the bill structure of Accipitres are connected with this function (Stresemann, 1929, p. 467). The widening of slits plays in certain cases a part in the chopping up of food – as a matter of fact it also plays a part in other functions – we cannot however, indicate one certain peculiarity in the structure of the bill for this function, for, in Aves, Nature has realized four different solutions for this action (Stresemann, 1929, p. 439).

As regards the accessory functions of the bill of Birds, which are accompanied by certain peculiarities in the structure of the upper bill, we want to point out the following cases. The bill of *Licmetis* is a long digging rod ("Grabstock") (Stresemann, 1929, p. 463); the upper bill of *Lophophorus* has become a digging spade ("Grabschaufel") (Stresemann, 1929, p. 469; Böker, 1937, p. 25). The broad bill of Anatinae serves as a sieve (see my fig. 52). The hook of the relatively short upper bill of most Psittaci serves them in pulling themselves up when climbing (Stresemann, 1929, p. 463). In Rhamphastidae with their large – and at the same time vividly coloured – bills, and in Bucerotidae with their protuberances on the upper bill, we are reminded of an added function in courtship or other psychical manifestations ("in den Dienst der Werbung oder anderer Ausstrahlungen der psychischen Sphäre") (Stresemann, 1929, p. 484) (see my figs 15 and 69). The very large bills of Rhamphastidae and Bucerotidae may be nearly as large as the whole bird (Owen, 1866 II, p. 149; Marinelli, 1936, p. 810; Böker, 1937, pp. 104/105). We may also point out the enlargement of the volume of the upper bill by a bony excrescence on the upper bill, as in Casuariidae and Anserinae *etc.* (Marinelli, 1936, p. 810).

So we may conclude that the possible connection between the length of the bill and that of the body, is crossed by numberless possibilities, as Marinelli indicates.

In Mammalia the mastering and consumption of the food, in the sense of cutting it up, is the most striking function of the jaw, minimizing that of the taking of the food. It is true that Weber

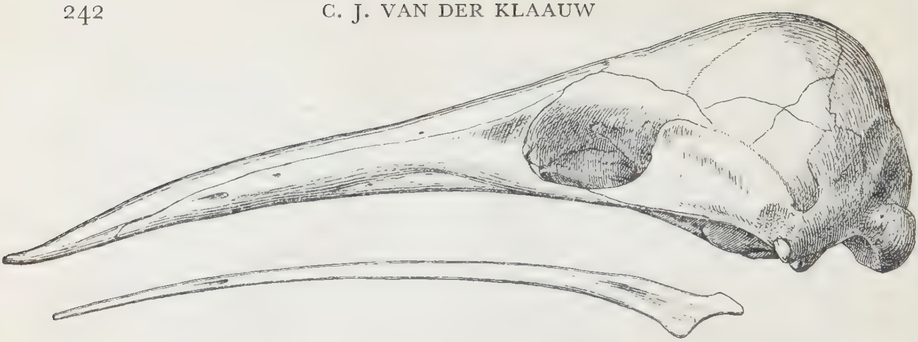
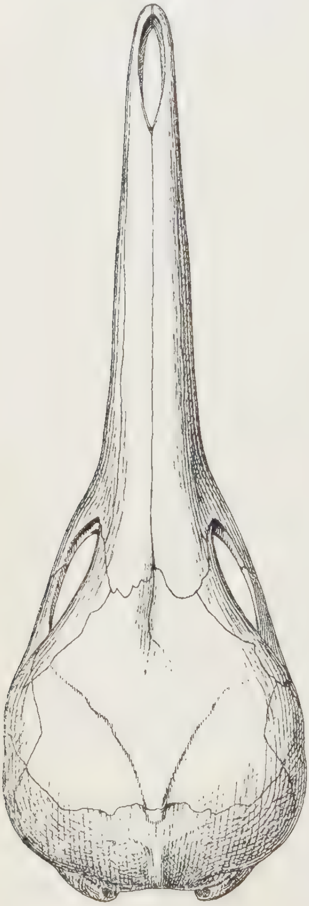


Fig. 107. *a. Zaglossus bruynii nigroaculeatus* (Rothschild). Skull seen from the left side. Zool. Mus. Amsterdam. 0.75×. Original drawing by M. A. Koekkoek.



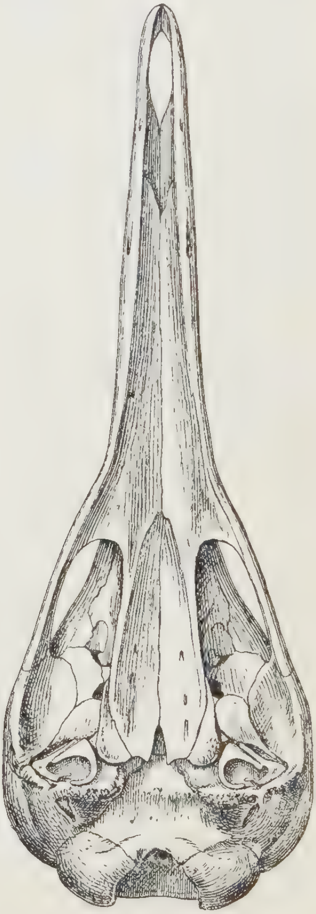
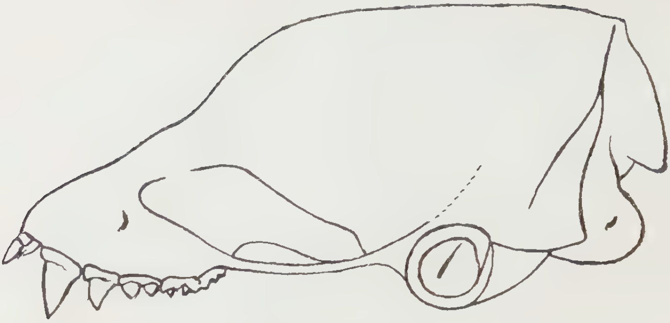


Fig. 107. *b. Zaglossus bruynii nigroaculeatus* (Rothschild). Skull seen from above. Zool. Mus. Amsterdam. 0.75×. Original drawing by M. A. Koekkoek.
Fig. 107. *c. Zaglossus bruynii nigroaculeatus* (Rothschild). Skull seen from below. Zool. Mus. Amsterdam. 0.75×. Original drawing by M. A. Koekkoek.

(1927 I, pp. 269, 327) regards the function of chewing as perhaps the most important acquisition ("Erwerb") of the Mammalia; by this entirely new ways to omnivory, frugivory and herbivory would have been opened, and by the manysidedness of the diet the great manysidedness in the development of the body and in the habitat has been rendered possible. Therefore in Mammalia the differentiation of the dentition, and the size and shape of the teeth has a great influence on the size, shape and solidity of the jaw, also in connection with the chewing pressure.

In insect- and worm-eaters among the Mammalia the task put on the jaw in the mastering and consumption of the food has become slight. The peculiarities in the structure of these Mammalia are, therefore, mainly connected with the taking of the food. For also in the Mammalia a long and narrow upper jaw combined with a mouth that can be opened widely is an advantage for a quick and sure grip on the prey. In Monotremata, Tubulidentata and Myrmecophagidae the jaws are strongly elongated (see my fig. 107). For the rest the upper jaws of Monotremata and of most Edentata, which are entirely or practically toothless, are very poorly developed (Stadtmüller, 1936, pp. 955, 964, 983, 984). In those Mammalia which seize insects and other small animals which live on the boughs of trees or on the earth, the skull is, according to Böker (1937, p. 105) narrow and pointed; in my opinion the great length and the slight breadth of the new upper jaw plays an important part here. In flying Mammalia which seize insects on the wing, we find, just like in Aves which catch their prey in this way, a very wide slit of the mouth and a short, broad skull (Böker, 1937, p. 107). Thus in insectivorous Microchiroptera, such as *e.g. Barbastella*, the face is broad and heavy and the head short and broad, connected with a shortened snout and a short but broad new upper jaw; at the same time the cerebral skull is shortened and rounded (Stadtmüller, 1936, p. 970; Böker, 1937, p. 107) (see my fig. 108). In Cetacea which also catch small animals which make no or slight demands on the chewing capacity of the jaws, and where the capacity to chew has even been lost, so especially in Mystacoceti, the mouth opening is also very large and the jaws are relatively very long, owing to the very great length of the maxillare. In consequence the facial skull is relatively strikingly long in proportion to the short, bullet-shaped, often very small cerebral skull; the great length of the jaws is accompanied by slight



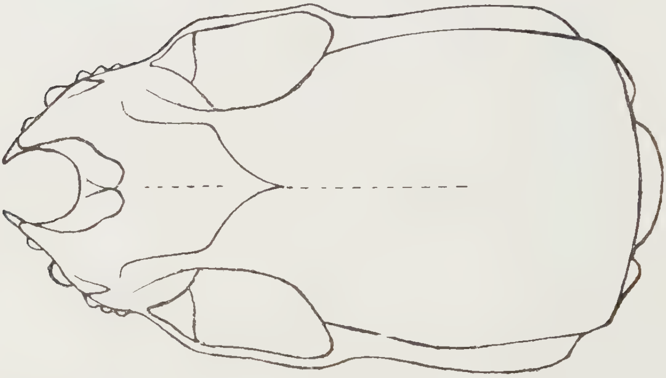
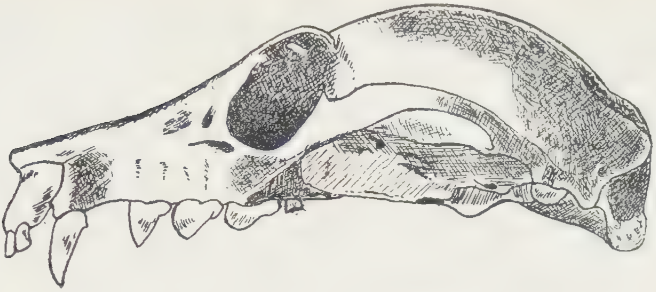


Fig. 108. *a. Barbastella barbastellus* (Schreber). Skull seen from the right side inverted. 6×. After G. S. Miller (1912), fig. 46 on p. 265.

Fig. 108. *b. Barbastella barbastellus* (Schreber). Skull seen from above. 6×. After G. S. Miller (1912), fig. 46 on p. 265.

breadth and height of the new upper jaws through which their volume is not very great (Owen, 1866 I, p. 249; Stadtmüller, 1936, pp. 933, 956, 958, 986, 987; Böker, 1937, p. 52). Still there are important differences in these respects among the Cetacea (see my figs 59, 70 and 110).

In the seizing and holding of larger animal prey the front elements of the teeth play an important part, and the development of the praemaxillare is connected with this. In this connection we want to point to the Carnivora. The catching, gripping and



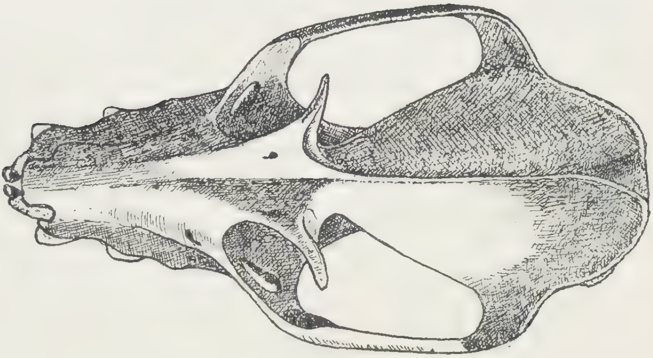


Fig. 109. *a. Pteropus lepidus* (Gervais) ♀. Skull seen from the left side. 1.35×. After G. S. Miller (1907), fig. 8 on p. 58.

Fig. 109. *b. Pteropus lepidus* (Gervais) ♀. Skull seen from above. 1.35×. After G. S. Miller (1907), fig. 8 on p. 58.

holding of a frantically struggling prey demands short, broad jaws, also in Mammalia (see my figs 148, 153, 154, 155).

Also in herbivorous Mammalia we find a short, broad upper jaw and snout. In frugivorous Megachiroptera, such as *e.g.* in *Pteropus*, we find a longer, more distended snout than in insectivorous Microchiroptera (Stadtmüller, 1936, p. 970; Böker, 1937, p. 107) (see my fig. 109).

In most Mammalia structure and shape of the new upper jaw is determined by the function of the mastering and consumption of the food, so by the chewing-function of the back-teeth, but also by the function of the front-teeth, insofar as they divide the food into smaller pieces. Through the development of this chewing-function the new upper jaw is relatively very voluminous. In this connection we point to the important differences in the structure of the teeth, and, connected with this, that of the new upper jaw in Carnivora with their powerful canini and carnassial teeth; in Rodentia with their powerful incisivi, whereas the canini are lacking, and in Ruminantia and Perissodactyla where the part of the jaw bearing the praemolares and molares is very powerfully developed (see my figs 8, 111, 112, 147–150, 152–155). Among the groups mentioned Ruminantia have no incisivi in the new upper jaw. Reduction of the incisivi in the new upper jaw, in connection with the fact that they have no part in the chopping up of the food – or in the seizing of the food or some other allied function – has very different consequences for the size of the praemaxillare. Sometimes reduction of the incisivi is accompanied by reduction of the praemaxillare, as *e.g.* in Edentata, with the exception of † Megatheriinae, especially † *Grypotherium etc.*, but in other cases the praemaxillare is little influenced by the reduction of the incisivi, as in Ruminantia and also in Mystacoceti (Stadtmüller, 1936, pp. 932, 981, 983, 985, 987). In herbivores the jaw is generally short. In the phytophagous Bradypodidae the new upper jaw is extremely short in contrast to the very long upper jaw of the insectivorous Myrmecophagidae (Stadtmüller, 1936, p. 984). In the omnivorous Primates the new upper jaw is relatively very short and the volume is also relatively small with regard to the very large cerebral skull; this is especially the case with *Homo* and a number of Pongidae where a protruding snout has disappeared completely or for the greater part (see my figs 46 and 113).

Also in Mammalia the accessory functions may influence the development of the new upper jaw. The fact that Carnivora use the canini as a weapon has its influence on the development of the jaw, the fact that the tusks of *Elephas* are used in the same way is responsible for a very great development of the praemaxillare wherein the alveolus of the tusk is situated; this alveolus, however, passes through the maxillare extending into the orbita (Stadtmüller, 1936, p. 978; Böker, 1937, pp. 34/35). In grubbing Mammalia, such as *Talpa*, *Condylura*, *Chrysochloris*, *Notoryctes*, *Geomys etc.*, the head is situated like a wedge on the cylindrical body (Böker, 1935, p. 174); the wedge-shape of the skull is connected with this, to which the shape of the snout principally contributes, which, in its turn is again connected with a certain development of the new upper jaw. Also in Suinae the skull is peculiarly wedge-shaped, which shape is characteristic for the skulls of all Suinae (BÖKER, 1937, p. 32); this is also principally due to the shape of the snout (see my fig. 49).

Owing to all these differences the relative size of the new upper

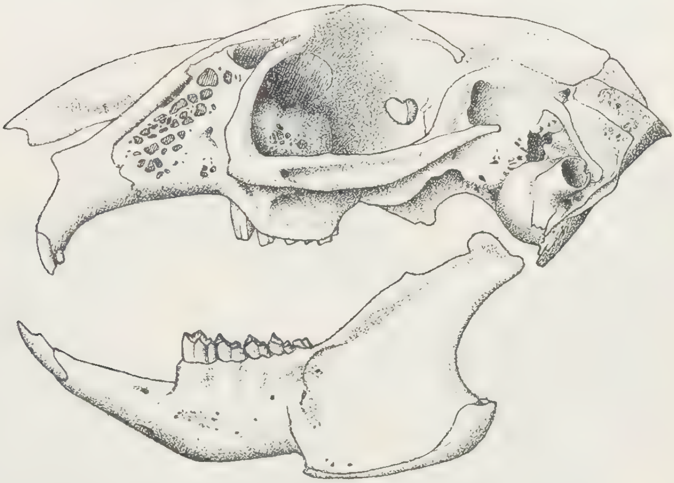


Fig. 111. *Lepus nigricollis* F. Cuvier. Skull seen from the left side. Zoöl. Mus. Buitenzorg, no. 1879. Nat. size. Original drawing by Mrs M. IDENBURG in the coll. of dr K.W. DAMMERMAN.

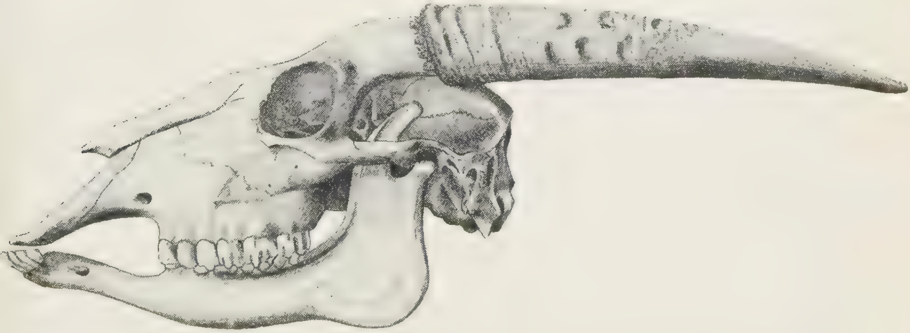


Fig. 112. *Anoa depressicornis* (Hamilton Smith). Skull seen from the left side. Zoöl. Mus. Buitenzorg, no. 762. 0.22 × . Original drawing by Mrs M. IDENBURG in the coll. of dr K. W. DAMMERMAN.

jaw diverges very much in Mammalia, although it does not diverge so much as in Sauropsida. We point out the differences mentioned above between Microchiroptera and Megachiroptera, between Myrmecophagidae and Bradypodidae. To this we may yet add that among Lemuroidea *Lemur* shows a snout lengthened like that of a beast of prey combined with an elongated cerebral skull, whereas in *Daubentonia* (*Chiromys*) and Lorisidae the facial skull is shortened and the cerebral skull strongly rounded (Stadtmüller, 1936, p. 988).

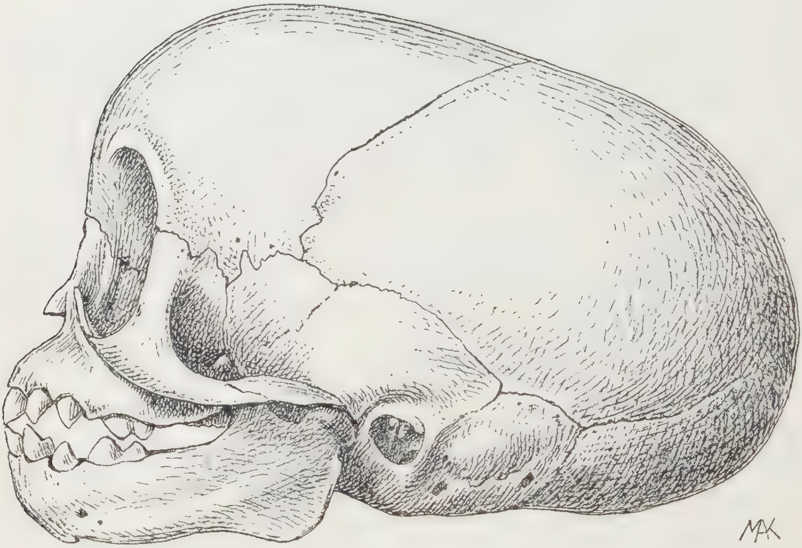


Fig. 113. *a. Nasalis larvatus* (Wurmb.). Juvenile. Skull seen from the left side. R.M.N.H. Leiden. 1.4×. Original drawing by M. A. Koekkoek.

The "facial angle" may give us an impression of the relative length of the upper jaw with regard to the height of the cerebral skull and at the same time of the mutual position of these two. This "facial angle" is, according to Owen (1866 II, p. 572) obtained "if a line be drawn from the occipital condyle along the floor of the nostrils, and be intersected by a second touching the most prominent parts of the forehead and upper jaw, the intercepted angle gives, in a general way the proportions of the cranial cavity and the grade of intelligence, it is called 'the facial angle'." Owen (*l.c.*, p. 572) gives the following values for this angle: *Canis familiaris* L. 20°, *Pongo pygmaeus* (Hopp.) 40° ("the prominent superorbital ridge occasions some exaggeration"), *Homo sapiens* L. 85°–95°. Whether Owen (1866 II, p. 318) means the same angle when he states that the facial angle in *Ornithorhynchus* is 20° and that in *Tachyglossus (Echidna)* 36°, may be doubted.

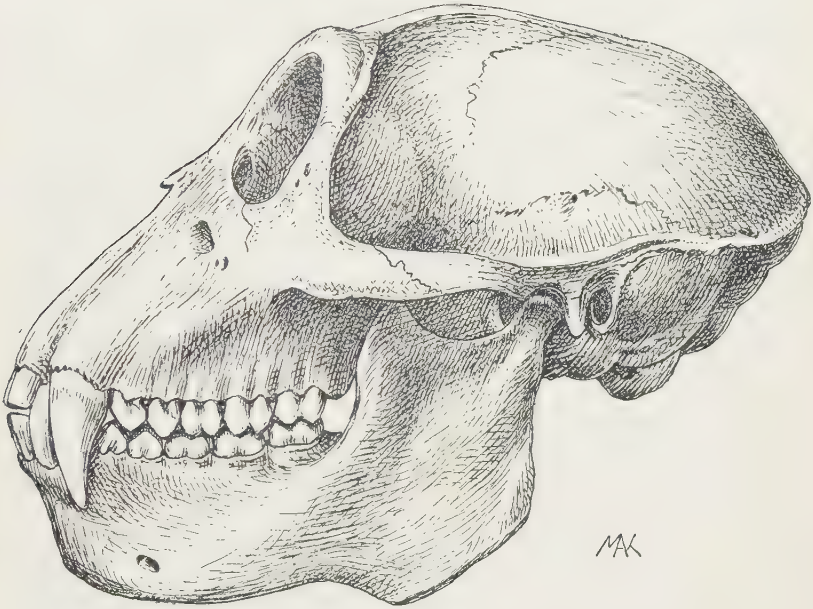


Fig. 113. *b. Nasalis larvatus* (Wurmb.). Adult. Skull seen from the left side. R.M.N.H. Leiden. 0.8×. Original drawing by M. A. Koekkoek.

In the above we have said in general that there is no direct connection between the length of the new upper jaw and that of the snout, because the snout is determined by the situation of the orbita, which can be situated far rostralward as well as far caudalward, so that the new upper jaw may extend more or less far below or behind the orbita. As regards the size of the snout we may refer to the information given above and here limit ourselves to the remark that in *Homo* and in *Rupicapra rupicapra* (L.) the snout is very short, in connection with the frontal situation of the orbitae, in *Homo* the new upper jaw is at the same time very short in connection with the decrease in the number of teeth and back-teeth (Böker, 1935, pp. 138, 148) [1]).

c. The position of upper jaw, upper bill, rostrum and snout

In contemplating the position of upper jaw, upper bill, rostrum and snout we must consider this situation with regard to the cerebral capsule, the nasal capsule and the orbita.

Before passing on to this discussion we want in the first place to draw the attention to the fact that in the Pisces with a movable upper jaw and in the Sauropsida with a kinetic skull the position of the new upper jaw and consequently of the snout, is not fixed but may modify itself.

With regard to the movable upper jaw in Pisces we limit ourselves to referring to the general remarks on the protrusility of the new upper jaw with its consequences for the position, as given by Gregory (1933, pp. 239–242), while at the same time we refer to the special mention of protrusility by Gregory for Ostariophysi, such as *Carpiodes* sp. (p. 424, see also p. 189), Acanthopterygii, such as *Scorpaena scrofa* L. (p. 424, see also p. 239), further for *Cyprinus carpio* L. and allied Eventognathi (pp. 190/191), *Fundulus* (p. 218), *Gasterosteus trachurus* C. & V. (p. 224), the Labridae (p. 256), *Epibulus* (p. 257), *Zeus* (p. 271), *Capros aper* (L.) (p. 272), *Antigonia capros* Lowe (p. 273). Finally we want to mention the term "Stülpmaul" used by Böker (1937, pp. 54/55) for certain Pisces.

As regards kinesis we only point out the changing position of the upper jaw in movements of the maxillary segment of the kinetic skull, which is especially clear in Serpentes (Ophidia) devouring a large prey, in doing which the two halves of the upper jaw are displaced separately (Böker, 1937, pp. 122, 135).

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[1]) For the increase of the relative length of the preorbital part in the phylogeny of Equidae, see: R. Cumming Robb (1935), J. Genetics **31**, pp. 39–46. (Postwar addition in the manuscript)

About the situation with regard to the cerebral capsule, there is in general not much to be said, except that the new upper jaw, the rostrum and the snout are practically always situated before the cerebral capsule.

In the primary platybasic skulls of Elasmobranchii, where the primary upper jaw is the one in use, this upper jaw is partly situated in front of, but for the greater part beside and below the rostral part of the cerebral capsule, not only because this latter stretches so far rostralward, but also because the opening of the mouth lies at a great distance behind the front point of the skull (see my fig. 61).

The primary rostrum of Elasmobranchii lies rostralward of the cerebral capsule (see my fig. 61).

As regards the slope of the primary rostrum with regard to the cerebral capsule we want to point to conditions as existing in *Acipenser* where the whole primary rostrum and fore part of the brain case is warped downward above the capacious orobranchial cavity in order to bring the rostrum down parallel to the ground; connected with this downward displacement of the rostrum, the ethmo-vomer block and also the interorbital bridge are drawn downward and forward, so that the lower surface of the ethmo-vomer block lies much below the level of the floor of the cranial vault (GREGORY, 1933, pp. 119, 438) (see my fig. 74).

The secundary rostrum in the sense as the term is used in this article, *viz.* an elongation of the snout, formed by allostoses, protruding before the frontal ridge of the new upper jaw, lies, on those grounds, rostral of the cerebral capsule.

As regards the slope of the secondary rostrum we point to conditions as existing in *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*) where the secondary rostrum in our sense, together with the snout is downbent and, as in *Acipenser*, is curved downward so as to project in front of the very small mouth (GREGORY, 1933, pp. 176, 177) (see my fig. 64).

In the higher Pisces the new upper jaw generally is also situated entirely or nearly entirely in front of the cerebral capsule. This is connected with the tropidobasity of the skull, by which the real cerebral capsule has been forced back caudally, and it is connected with the generally slight development of the praemaxillare and maxillare. We will not discuss this state of affairs exhaustively because we should then have to ask ourselves if and in how far we must ascribe upper jaw functions to praemaxillare and maxillare, because attention has seldom been drawn to their position, but also because more stress has been laid on their position with regard to the orbita. In the discussion of this latter position it will appear that in a number of cases the new upper jaw extends caudally of the orbita and, consequently, is situated ventrally of the cerebral capsule and may even extend caudally of this. We mention *Gastrostomus* where not only the snout is much shortened, but the whole skull is much shortened anteroposteriorly, while the jaws are enormously long (GREGORY, 1933, p. 213) (see my fig. 87).

Here we will discuss the slope of the new upper jaw and the snout in the higher Pisces with regard to the cerebral capsule, as far as GREGORY (1933) furnishes us with data. In certain Mormyridae, as in *Gnathonemus curvirostris* Blgr., the long snout is decurved (GREGORY, 1933, pp. 171, 417) (see my fig. 66). In *Microspathodon* and in Labridae the snout shows a downward prolongation (pp. 255, 256). *Capros aper* (L.) shows a great downward and forward prolongation of the praemaxillare (p. 273). Owing to a marked shortening of the snout especially, which in itself brings the dorsal border of the mouth to a higher level, the tip of the upper beak in *Lagocephalus* is almost in horizontal line with the basis cranii, whereas in the small-mouthed nibbling fishes such as the Siganidae (Teuthidae) and Balistidae, the upper jaw is far beneath the level of the basis cranii (GREGORY, 1933, p. 290) (see my fig. 43).

In the primary platybasic Amphibia, where the cerebral capsule extends far rostralwards, the very long new upper jaw lies, for a considerable part beside the cerebral capsule. The snout, situated according its definition, preorbitally, lies at the same time practically entirely precerebrally.

In Reptilia the new upper jaw is situated in front of the cerebral capsule. This is connected with the tropidobasity, owing to which the cerebral capsule proper is displaced caudally, but it is also connected with the smallness of the cerebral capsule. Whether, and in how far the back part of the new upper jaw extends below the cerebral capsule should be investigated. In Reptilia the snout, as a preorbital formation, lies, in these tropidobasic skulls, at the same time precerebrally.

In Aves the upper bill also lies in front of the cerebral capsule, which is again connected with the tropidobasity. As regards the slope of the upper bill with regard to the cerebral capsule, we must observe that in the straight type of bird skull the direction of the basis cranii roughly agrees with the axis of the bill, whereas in the curved or cracked type of bird skull the axis of the brain is always steeply raised with regard to the bill and the under surface of the brain is turned more or less towards the front (MARINELLI, 1936, p. 811) (see my figs 13 and 14). In Picidae where the bill acts as a chisel the deflection ("Abknickung") of the axis of the upper bill with regard to the axis of the basis cranii is very slight (STRESEMANN, 1934, p. 842). This ventrally directed deflection of the facial skull is an advantage when exercising pressure in biting, cutting-up and sawing ("Zerschneiden" and "Zersägen") and also in pecking things from the ground; this deflection also causes modifications in the relations between the field of vision, and the field of activity of the bill (GROEBBELS, 1932, p. 402).

If the term "snout" should be used in connection with Aves, it would, according to definition, have a preorbital position, and, consequently, also a precerebral one in these tropidobasic skulls with a caudally displaced cerebral capsule proper.

In Mammalia a great part of the new upper jaw has nearly always a precerebral situation. The new upper jaw extends as far as below the orbita or it even extends further caudally and, seeing that, in these secondary platybasic skulls the orbita is situated beside the front part of the cerebral capsule, this indicates at the same time how far the new upper jaw extends with regard to the cerebral capsule. I have, however, not found any precise data in literature about the situation of the back edge of the new upper jaw with regard to the cerebral capsule. The situation of the front edge of the new upper jaw with regard to the cerebral capsule is better-known, because it is closely connected with the length of the snout. By the side of very long snouts we also meet with very short ones in Mammalia. Thus the bony snout of Proboscidea protrudes very little, also, the skull as a whole is short, but very high and broad (STADTMÜLLER, 1936, p. 978). In Primates the new upper jaw does not protrude very much in front of the cerebral capsule and sometimes it is for a considerable part, or even entirely, subcerebral (see my figs 5, 16, 46 and 113). In Cetacea the upper jaw may protrude very much in front of the cerebral skull (STADTMÜLLER, 1936, p. 956).

However, as regards the question of the mutual situation of new upper jaw and cerebral capsule, many differences are found in closely related species, in different races and local forms of identical species and in different stages of the ontogenics of a special species, indeed, even in senile forms as opposed to adult ones, and in the skulls of the two sexes, as well (OWEN, 1866 II, p. 534; DUBOIS, 1917, pp. 282, 283; STADTMÜLLER, 1936, pp. 956, 991). Especially in *Homo sapiens* L. these points have been exhaustively examined. The variations in the shape of the skull in connection with the age is strongest in Primates, slightest in Carnivora (KINGSLEY, 1925, p. 186).

As regards the slope of the new upper jaw with regard to the cerebral capsule we find that, also in Mammalia, it is among other things determined by the size of the angle of the crack or curve in the basicranial axis. This crack or curve is lacking in Mesaxonia, but it occurs in Artiodactyla, and it is most strongly developed in Cavicornia; the occurrence of a facial hiatus ("Ethmoidallücke (Gesichtslücke)"), which may separate maxillare and lacrimale, must be connected with this deflection (STADTMÜLLER, 1936, pp. 979, 981).

As regards the situation of the new upper jaw and snout with regard to the nasal capsule we may refer to the discussion of this situation in the paragraph on the nasal capsule. The extension of the new upper jaw in a more caudal direction will be discussed beneath.

The proximal end of the primary rostrum of Elasmobranchii is situated between the two nasal capsules, but it extends, for the greater part in a more rostral direction (see my fig. 61).

The situation with regard to the orbita has seldom been examined.

The primary rostrum of Elasmobranchii lies in the ethmoidal region, and preorbitally.

The secondary rostrum, in the sense as the term is used here, also lies preorbitally.

According to its definition the situation of the snout is preorbital, too.

The situation of the new upper jaw with regard to the orbita is seldom especially mentioned in the literature I worked through.

In Elasmobranchii the old upper jaw which serves as upper jaw, reaches behind the orbita, the pars quadrata being suspended behind the orbita, auto-, hyo-, or amphistyllically (see my figs 61 and 62).

In the higher Pisces, too, we have here to deal with the difficulty if and in how far the praemaxillare and maxillare perform the functions of an upper jaw. Seeing that in the above we often could not come to a definite conclusion on this point and had to be satisfied with a greater or lesser probability, even with mere possibilities, we shall refrain from giving an exhaustive enumeration of all that may be inferred from the illustrations given by GREGORY (1933), about the situation of the upper jaw with regard to the orbita. We want to stress mainly what GREGORY mentions in his text.

The situation of the upper jaw with regard to the orbita in the higher Pisces is most closely connected with two factors; first with the proportion of the length of the upper jaw to the length of the snout, and, secondly with the vertical distance between the quadratum-articulare joint and the horizontal through the ventral border of the orbita (see my fig. 114). A long upper jaw combined with a short snout does not simply mean that the upper jaw protrudes behind the orbita, this is *viz.* not the case when the quadratum-articulare joint is situated very far ventral of the orbita. When we take this second factor into consideration we shall be able to use the four main types of the proportion between the length of the upper jaw and that of the snout, mentioned above, here too (p. 220).

In the first main type (snout long, upper jaw short) the upper jaw, also the new upper jaw which lies at the end of the long snout, remained rostral of the orbita. For examples we refer to the discussion of this main type given above (see my figs 43, 66, 91, 93, 117 and 118).

In the second main type (snout long, upper jaw long) there are in principle three possibilities: the upper jaw remains entirely in front of the orbita; the upper jaw reaches below the orbita and the upper jaw reaches even farther caudalward past the back ridge of the orbita. An example of the first possibility is *Anableps tetrophthalmus* Bl. where the new upper jaw lies wholly in front of the orbita (p. 220, fig. 98) (see my fig. 40) and farther, according to the illustrations in GREGORY in *Lepisosteus* (fig. 24) (see my figs 51 and 65), *Albula vulpes* (L.) (fig. 37 A) (see my fig. 125), *Tylosurus marinus* (Walbaum) (fig. 99) (see my fig. 94), *Tautogolabrus adspersus* (Walbaum) (fig. 129) (see my fig. 81), *Istiophorus* (fig.

196), *Echeneis* (fig. 199), *Prionotus evolans* (L.) (fig. 218), *Trigla hirundo* Bl. (fig. 219), *Mastacembelus* (fig. 233), and *Parachaenichthys georgianus* (Fischer) (fig. 239 C). In the second case the upper jaw extends below the orbita, as in † *Furo* (*Eugnathus*) (fig. 27), *Esox masquinongy* Mitchill (fig. 95 A) (see my fig. 30), *Haemulon* (fig. 121) (see my fig. 127), *Lachnolaimus maximus* (Walbaum) (fig. 130) (see my fig. 129), *Sphyraena barracuda* (Walbaum) (fig. 141) and *Rhachycentron* (fig. 186) (see my fig. 120). I have not met with an example of the third possibility.

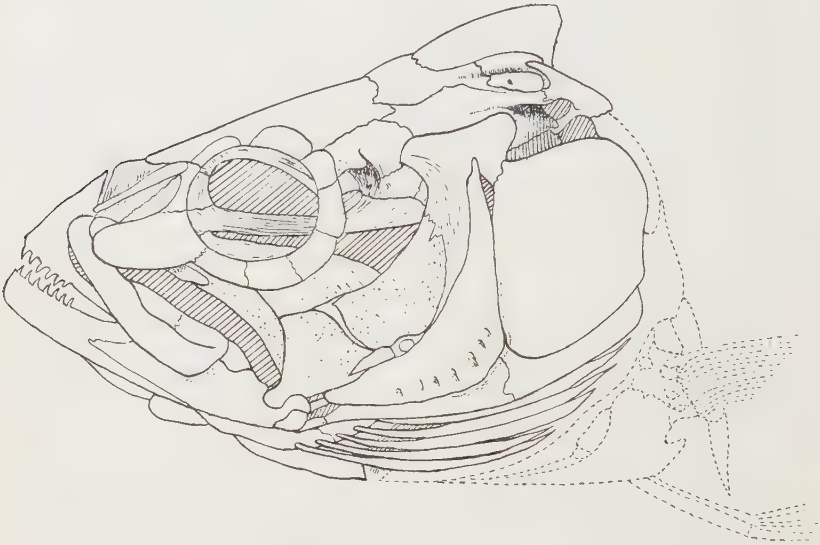

Fig. 114. Diagram of a teleost skull. Skull seen from the left side. After GREGORY (1933), fig. 7 on p. 87.

In the third main type (snout short, upper jaw long) a new upper jaw that ends already rostralward of the front edge of the orbita, will not be met with. We only find the new upper jaw ending ventral of the orbita or extending caudal of the orbita. A new upper jaw that ends ventral of the orbita will only be found in this third main type when the quadratum-articulare joint lies at a considerable distance ventral of the orbita, as is the case in *Chauliodus sloanei* Bl. Schn. (fig. 55) (see my fig. 122), *Lates niloticus* (Gmel.) (figs 114, 298) (see my fig. 115), *Polydactylus* sp. (fig. 144), *Aspicottus* (*Enophrys*) (fig. 216), *Trachinus* (fig. 243), *Fierasfer* (fig. 257) (see my fig. 146), *Opsanus tau* (L.) (fig. 263 A) and *Antennarius* (fig. 265). But in most cases the new upper jaw extends caudalward of the back edge of the orbita. We may here distinguish three cases: it may be combined with a raised situation of the quadratum-articulare joint with regard to the orbita, thus with a small vertical distance between the two, in the second place this vertical distance may be considerable, with all the gradual transitions between these two cases and in the third place other circumstances may play a part *viz.* the caudalward continuation of the maxillare past the quadratum-articulare joint, as is the case

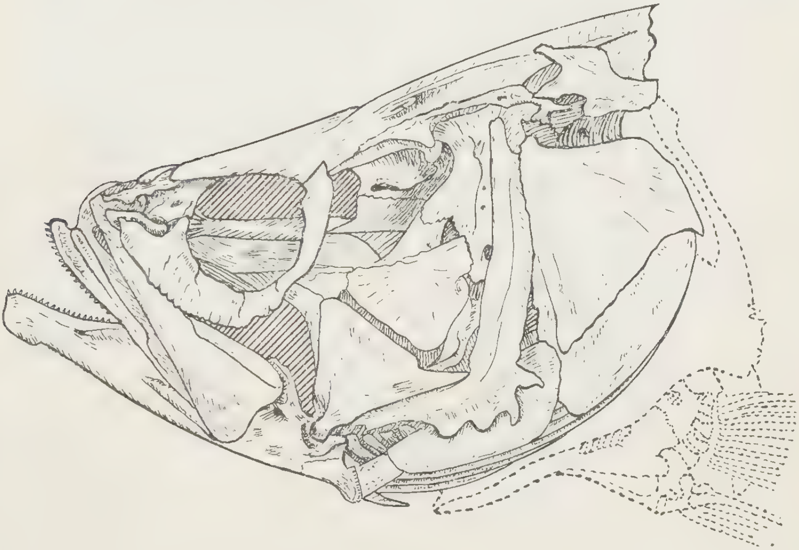

Fig. 115. *Lates niloticus* (Gmel.). Skull seen from the left side. After GREGORY (1933), fig. 114 on p. 239 and fig. 298 on p. 434.

in *Tarpon atlanticus* (C. & V.) (fig. 31) (see my fig. 85). If the quadratum-articulare joint is raised with regard to the orbita, the upper jaw runs, roughly, horizontal. We find this in † *Cheirolepis trailli* Agassiz, where a good part of the new upper jaw lies behind the orbiton, *i.e.* the most anterior point of the orbita, but also behind the back edge of the orbita (pp. 85, 421; figs 12 A, 283 A, 286 A) (see my fig. 95). We also find this in the allied Palaeoniscidae † *Palaeoniscus macropomus* Agassiz (fig. 12 B) and † *Coccocephalus wildi* Watson (figs 12 C, 283 B, 286 B). According to the illustrations in GREGORY we also find this condition in *Stomias boa* (Risso) (fig. 56), *Lycodontis funebris* (Ranzani) (fig. 82 B) (see my fig. 119) and *Synodus foetens* (L.) (fig. 86). According to GREGORY (1933, p. 268, fig. 144) the condition in *Polynemus* shows a convergent resemblance to the conditions in primitive † Palaeoniscidae, but the quadratum-articulare joint shows a downward and backward displacement so that in the illustration referred to, the new upper jaw hardly protrudes behind the orbita. When the vertical distance from the quadratum-articulare joint to the horizontal of the orbita is considerable, the back edge of the new upper jaw may reach caudal of the back edge of the orbita, we might almost say, in spite of this very ventral situation. The distance may be more or less great. It is very great in *Gastrostomus* (fig. 94) (see my fig. 87), but also in *Gonostoma elongatum* Gthr (fig. 53), *Osteoglossum* (fig. 57) (see my fig. 116), *Saurus myops* (Bl. Schn.) (fig. 87 A) and *Symbranchus* (fig. 231) (see my fig. 123). The new upper jaw extends less far caudalward of the back edge of the orbita in *Polypterus*, where the enlarged maxillare has apparently invaded the area of the suborbital series (p. 110, fig. 10). A similar, slighter extension is also found in *Amia calva* L. (fig. 28), *Salmo* (fig. 45), *Notopterus* sp. (fig. 61), *Erythrinus unitaeniatus* Spix (fig. 67) (see my fig. 28), *Myctophum humboldti* (Risso) (fig. 93), † *Hoplopteryx lewesiensis* (Mantell) (fig. 110), *Chiasmodon* (fig. 137) and *Ophicephalus* (fig. 145 A).

In the fourth main type (snout short, upper jaw short) the back edge of the new upper jaw remains rostral of the front edge of the orbita, as in *Eigenmannia macrops* (Blgr.) (fig. 73 A) (see my fig. 80), *Iniistius* (fig. 132) (see my fig. 128) and *Pelor japonicum* C. V. (fig. 206) (see my fig. 124); this back edge hardly reaches the front edge of the orbita as in † *Portheus molossus* Cope (figs 36, 288 B); or the back edge of the new upper jaw clearly extends a good bit below the lower edge of the orbita as in *Periophthalmus* (fig. 228) (see my fig. 41). In this connection we may also mention *Spheroides* where the entire palato-metapterygoid tract lies beneath the orbita, but the new upper jaw remains rostral of it (p. 289, fig. 167), and also *Petrocephalus bane* (Lac.), where the mouth lies beneath the orbita and where the new upper jaw extends ventral of the orbita as well (pp. 171–173, fig. 64) (see my fig. 88).

To this we will add data about the slope of the upper jaw. Properly speaking they belong to the situation of the upper jaw with regard to the cerebral capsule, but as the situation of the axis of the base of the skull is not known, while, on the other hand, in a great number of cases the slope of the upper jaw is connected with the situation of the orbita, we will add these data on the slope of the upper jaw in the higher Pisces here.

By the slope of the upper jaw we understand the angle of the gape, that is the inclination of the line of the gape either to the horizontal or to a line parallel with the horizontal, or in other words, the maxillary angle of the closed mouth is the inclination of the alveolar border of the upper jaw (projected in a parasagittal plane) to the horizontal axis of the body (Gregory, 1933, p. 420).

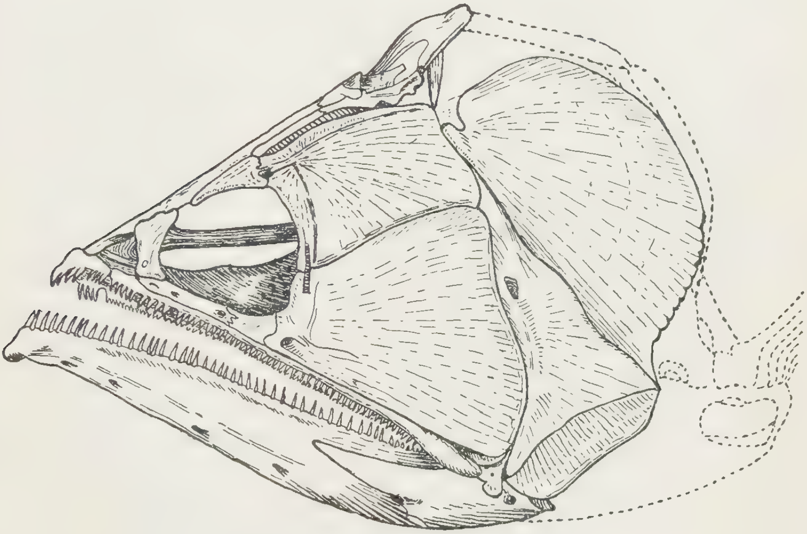

Fig. 116. *Osteoglossum.* Skull seen from the left side. After Gregory (1933), fig. 57 on p. 163.

In the definition the line of the gape is equal to the line of the quadratum pivot, (*i.e.* the mid-point of the articular hinge of the quadratum) either to the prosthion (*i.e.* the most anterior point of the snout) or to the praemaxillon or praemaxillare tip (*i.e.* the most anterior point of the praemaxillare in norma lateralis), whereby the prosthion and praemaxillon often coincide. The horizontal is the line, joining the prosthion and the pygidion (*i.e.* the mid-point of the narrowest part of the caudal peduncle) (Gregory, 1933, p. 420).

In the following we shall here and there refer to the direction and the slope of the mouth opening, but we shall not enter upon this very fully. The direction and the slope of the mouth opening are not only influenced by the slope of the upper jaw, but also by a number of other factors, such as the development of a rostrum, a beak, whether there is a prolongation of the praemaxillare *etc. etc.* (GREGORY, 1933, pp. 416/417, 428, 445; also pp. 250, 273).

With regard to the slope of the upper jaw which is connected with the orbita, we can distinguish three main classes of cases.

A. The entire upper jaw is situated caudal of the orbita, which is made possible by the fact that the upper jaw is not in any way attached to the neurocranium, which ends in a primary rostrum. The mouth opening will be directed downward, as is the case in *Acipenser* (GREGORY, 1933, p. 416) or at most rostralward (see my fig. 74). In connection with this the upper jaw points downward, too, or it is horizontal.

As examples of this main class A we refer to the pictures of *Acipenser* (GREGORY, 1933, fig. 19 A, see also, however, fig. 20) (see my fig. 74) and that of † *Chondrosteus* (fig. 19 B).

B. The upper jaw lies entirely rostral of the orbita, as is the case in the above-treated first main type of the proportion between the length of the snout to the length of the jaws, in which main type the snout is long and the jaws are short.

A horizontal lower edge of the upper jaw occurs in *Lagocephalus laevigatus* (L.), where the mouth has a terminal position (p. 292, fig. 168), and in *Zanclus cornutus* (L.) (fig. 158) (see my fig. 117).

In other cases the lower edge of the upper jaw slopes slightly more upwards, as in *Lactophrys tricornis* (L.) where the mouth itself is tilted partly downward, because the mouth has been brought down to the ventral border of the downwardly elongated snout (p. 286, fig. 166) (see my fig. 118) and in *Gasterosteus spinachia* L. (fig. 103), *Triacanthus* (fig. 160) and *Spheroides stictonotus* (Temm. & Schl.) (fig. 167).

A much stronger upward slope in the lower edge of the upper jaw is found in *Fistularia*, for which an upturned mouth is mentioned (p. 438, figs 105, 289 B) (see my fig. 93), in *Fundulus*, where the mouth is also upturned, pointing more or less upward (pp. 216, 221, 223, 416, fig. 96), in *Gasterosteus aculeatus* L. (fig. 102), *Aulostomus maculatus* Val. (fig. 104), *Phyllopteryx foliatus* (Shaw) (fig. 106), *Solenostomus* (fig. 107), *Angelichthys ciliaris* (L.) (fig. 153), *Pomacanthus arcuatus* (L.) (figs 154, 290 A), *Teuthis virgata* (C. V.) (fig. 159), *Balistes carolinensis* Gmel. (fig. 161) (see my fig. 43), *Alutera scripta* (Osbeck) (figs 163, 290 C) (see my fig. 91) and *Xesurus* (fig. 290 B).

In all these cases we have to deal with representatives of the above-mentioned first main type with long snouts and short jaws. But the lower edge of the upper jaw also runs horizontal in *Tautogolabrus adspersus* (Walbaum) one of the Labridae belonging to the second main type (snout long, jaws long), showing itself a horizontal mouth (p. 256, fig. 129) (see my fig. 81).

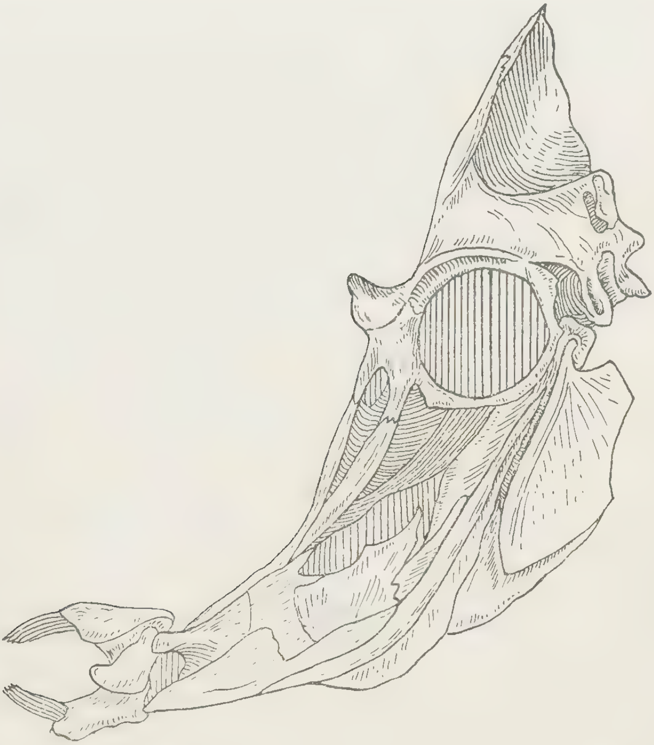

Fig. 117. *Zanclus cornutus* (L.). Skull seen from the left side. After GREGORY (1933), fig. 158 on p. 281.

C. The upper jaw lies partly below the orbita because the quadratum-articulare joint lies ventral or caudal of the orbita.

Some of GREGORY's observations (1933, p. 420) as a matter of fact only refer to this main class C, *viz.* when he says that a lengthening of the distance between the prosthion and the projection of the quadratum pivot upon the horizontal will decrease the angle of the gape (fig. 289), while a shortening of this distance will increase the angle of the gape (fig. 287 C), the vertical distance of the quadratum pivot to the horizontal being thought of as unaltered (see my fig. 114). A raising of the quadratum pivot with shortening of the distance between the quadratum pivot and its projection upon the horizontal will, according to GREGORY (1933, p. 421) decrease the angle of the gape (fig. 287 D, 286 D), while a lowering of this point will increase the angle of the gape (figs 288 B, D), the distance between the prosthion and the projection of the quadratum pivot on the horizontal, evidently being thought of as unaltered.

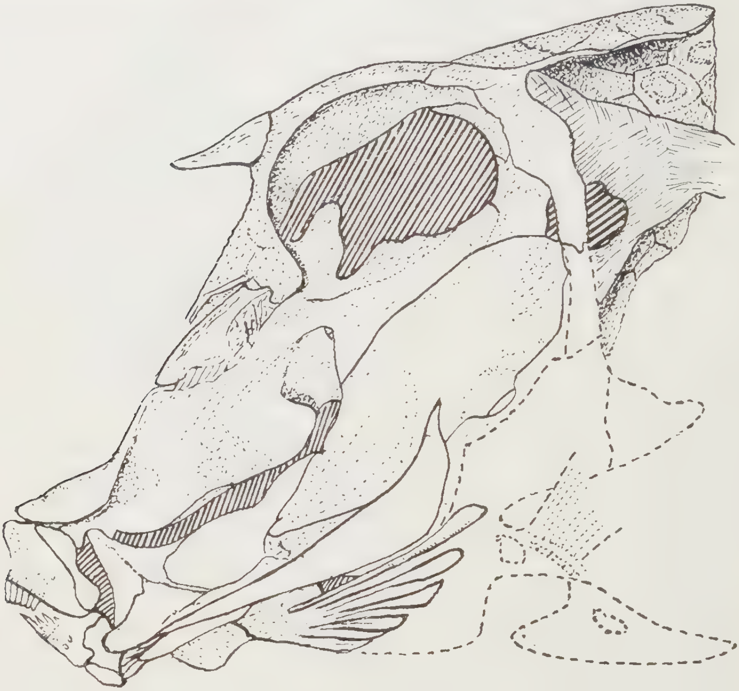

Fig. 118. *Lactophrys tricornis* (L.). Skull seen from the left side. After GREGORY (1933), fig. 166 on p. 288.

In the classification of the cases the length of the snout plays a part as well as the situation of the quadratum-articulare joint. We know, however, that the lower edge of the new upper jaw by no means always runs parallel to the line of the gape, and, consequently does not run into this joint, but, *e.g.* crosses the lower jaw rostral of the quadratum-articulare joint.

We shall take together the cases belonging to one main type of the proportion between the length of the snout to the length of the jaw.

We can then distinguish the following possibilities in our main class C.

a) The snout is short in a longitudinal direction and the quadratum-articulare joint lies far dorsally. Owing to this the lower edge of the new upper jaw runs practically horizontal and the mouth is terminal.

We find this condition in the following cases, all belonging to the third main type (jaws long, snout short): † *Cheirolepis trailli* Agassiz, of which it is said that the mouth is almost terminal and directed slightly upward (p. 416, figs 12 A, 283 A, 286 A) (see my fig. 95), in † *Palaeoniscus macropomus* Agassiz (fig. 12 B), † *Coccocephalus wildi* Watson (figs 12 C, 283 B, 286 B), *Stomias boa* (Risso) (fig. 56), *Lycodontis funebris* (Ranzani) (fig. 82 B) (see my fig. 119) and *Synodus foetens* (L.) (fig. 86).

In † *Pholidophorus macrocephalus* Agassiz, however, which also belongs to the third main type, the mouth is directed partly upward and the lower edge of the new upper jaw has an upward direction, too, because the orbita has a pronounced ventral situation (p. 136, fig. 29).

b) The snout is long in a longitudinal direction and the quadratum-articulare joint lies far dorsally. Therefore the lower edge of the new upper jaw runs horizontal and the mouth is, in general, terminal.

We find this condition in the following cases from the second main type (jaws long, snout long): *Lepisosteus* (figs 24, 287 D) (see my fig. 65), *Rhachycentron* (fig. 186) (see my fig. 120), *Mastacembelus* (fig. 233) and *Parachaenichthys georgianus* (Fischer) (fig. 239 C), while in *Tylosurus marinus* (Walbaum) the mouth points more or less upward (p. 223, figs 99, 289 A, 291 E) (see my fig. 94), which is certainly the case in *Anableps tetrophthalmus* Bl. (fig. 98) (see my fig. 40), *Sphyraena barracuda* (Walbaum) (fig. 141) and *Echeneis* (fig. 199).

c) The snout is short in a longitudinal direction but shows a downward prolongation and the quadratum-articulare joint is far dorsal. The lower edge of the new upper jaw is inclined downward and the mouth opening is ventral.

Of this possibility I have not found any examples.

d) The snout is short in a longitudinal direction and the quadratum-articulare joint has a clearly ventral situation, that is to say, there is a considerable distance between the quadratum-articulare joint and the horizontal through the ventral border of the orbita. Consequently the lower edge of the new upper jaw has an upward slope, and there is a tendency for the opening of the mouth to be upturned.

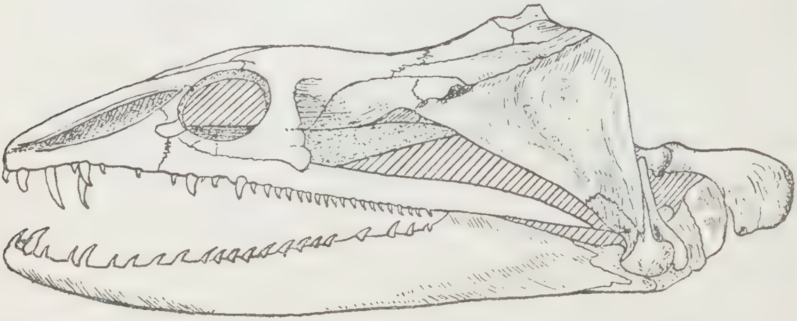

Fig. 119. *Lycodontis funebris* (Ranzani). Skull seen from the left side. After Gregory (1933), fig. 82 B on p. 202.

We find this in one case, derived from the first main type (jaws short, snout long) *viz.* in *Diodon hystrix* L. (fig. 170) (see my fig. 121).

We find this in a great number of cases belonging to the third main type (jaws long, snout short). In the following enumeration we shall keep to the classification into three types mentioned above, according to the degree to which the back edge of the new upper jaw extends caudally.

Among the cases where the new upper jaw ends ventral of the orbita because the quadratum-articulare joint lies at a considerable distance ventral of the orbita, the above-mentioned case d) occurs in *Chauliodus sloanei* Bl. Schn., where the mouth is superior and directed upward (p. 416, fig. 55) (see my fig. 122), *Trachinus*, where the mouth is said to be directed somewhat upward (p. 363, fig. 243), *Opsanus tau* (L.), where the mouth is superior and directed upward (p. 416, fig. 263 A) and *Antennarius*, where the mouth shows a sharp upward inclination (p. 390, fig. 265 A), further in *Lates niloticus* (Gmel.) (figs 114, 298) (see my fig. 115), *Polydactylus* sp. (fig. 144), *Aspicottus* (*Enophrys*) (fig. 216) and *Fierasfer* (fig. 257).

Among the cases where the back edge of the new upper jaw extends exceptionally far caudalwards, the following genera and species belong to this group d): *Gastrostomus* (p. 418, fig. 94) (see my fig. 87), further *Gonostoma elongatum* Gthr (fig. 53), *Osteoglossum* (fig. 57) (see my fig. 116), *Saurus myops* (Bl. Schn.) (fig. 87 A) and *Symbranchus marmoratus* Bl. (fig. 231) (see my fig. 123).

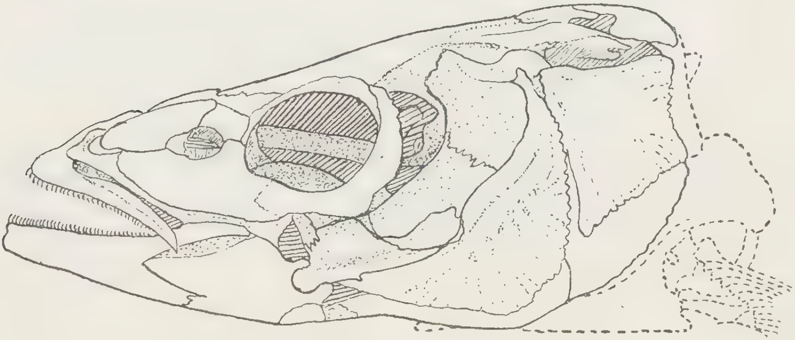

Fig. 120. *Rhachycentron.* Skull seen from the left side. After GREGORY (1933), fig. 186 on p. 308.

Between the two extremes mentioned, we find those cases where the back edge extends less far caudalwards of the back edge of the orbita, of these the following cases belong to this group d): † *Hoplopteryx lewesiensis* (Mantell) where the mouth opening is said to slope gently upward (p. 233, fig. 110), further *Polypterus* (fig. 10), *Amia calva* L. (fig. 28), *Salmo* (fig. 45), *Notopterus* sp. (fig. 61), *Erythrinus unitaeniatus* Spix (fig. 67) (see my fig. 28), *Myctophum humboldti* (Risso) (fig. 93), *Chiasmodon* (fig. 137) and *Ophicephalus* (fig. 145 A).

Tarpon atlanticus (C. & V.) diverges somewhat from this group by the peculiar shape of the caudal extension of the maxillare, all the same it also belongs to this third main type; it shows a marked uptilting of the jaws and a strongly upturned mouth (p. 138, fig. 31) (see my fig. 85).

To this group d) also belong some cases from the fourth main type (jaws short, snout short) such as *Pelor japonicum* C. V., where the new upper jaw lies practically vertical and the mouth is pushed upward and backward and opens upward (pp. 329, 417,

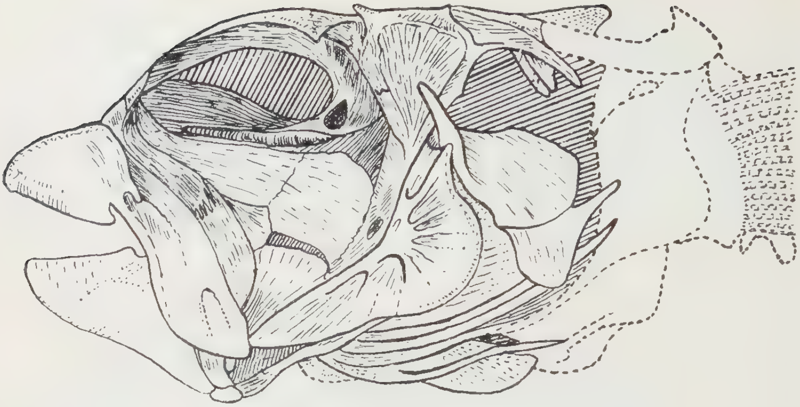

Fig. 121. *Diodon hystrix* L. Skull seen from the left side. After GREGORY (1933), fig. 170 on p. 292.

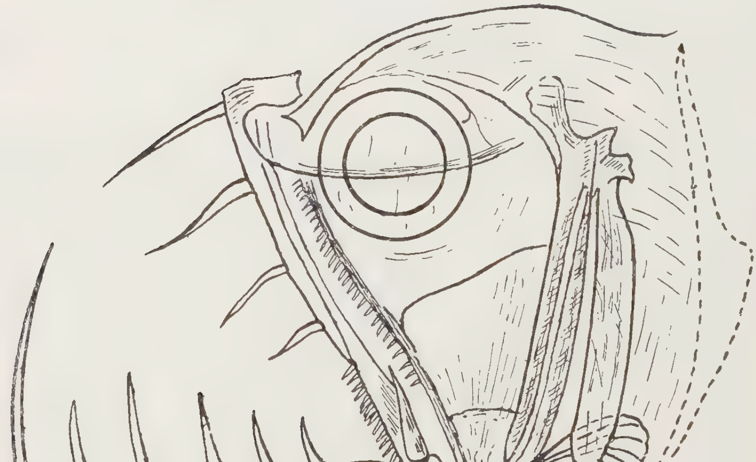

Fig. 122. *Chauliodus sloanei* Bl. Schn. Skull seen from the left side. After GREGORY (1933), fig. 55 on p. 162.

438, fig. 206) (see my fig. 124), then *Synanceja horrida* (L.), of which the jaws and mouth are directed sharply upward (pp. 329, 417, fig. 207) and † *Portheus molossus* Cope, where the new upper jaw has a sharp upward tilt and the mouth shows a sharp upturning (pp. 144, 416; figs 36, 288 B).

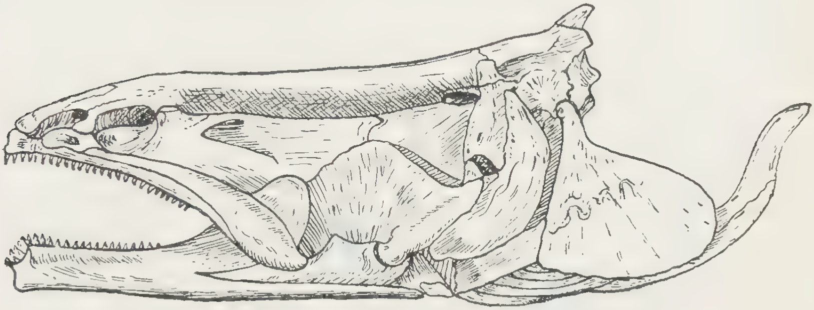

Fig. 123. *Symbranchus marmoratus* Bl. Skull seen from the left side. After Gregory (1933), fig. 231 on p. 351.

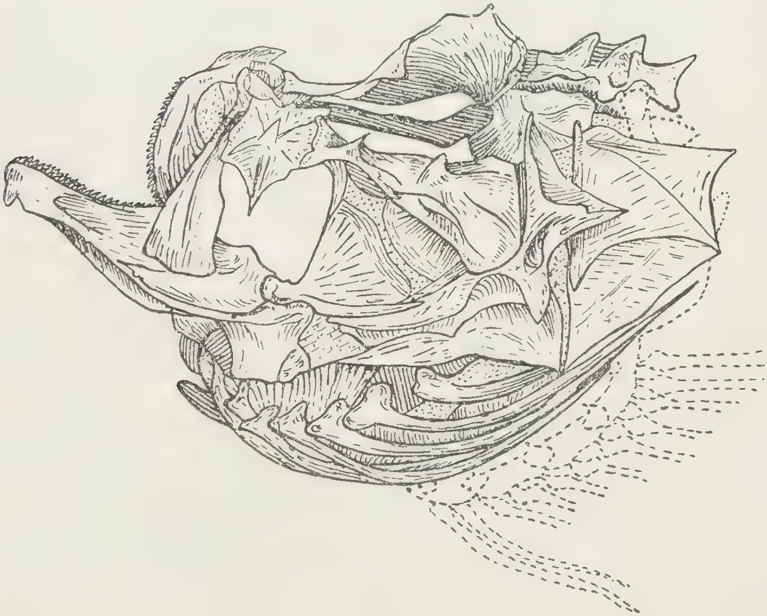

Fig. 124. *Pelor japonicum* C.V. Skull seen from the left side. After Gregory (1933), fig. 206 A on p. 328.

e) The snout is long in a longitudinal direction and the quadratum-articulare joint lies far ventralward. Therefore we may expect that the upper jaw slopes, but not exceptionally so.

This is the case in the following cases from the second main type (jaws long, snout long): *Albula vulpes* (L.) (fig. 37 A) (see my fig. 125) and *Esox masquinongy* Mitchill (fig. 95 A) (see my fig. 30).

In other cases, also from the second main type, this slope of the lower edge of the new upper jaw is stronger because the new upper jaw crosses the upper jaw rostral of the quadratum-articulare joint. This slope is fairly strong in *Trichiurus lepturus* L. (fig. 195), less strong in *Prionotus evolans* (L.) (fig. 218) and *Trigla hirundo* Bl. (fig. 219).

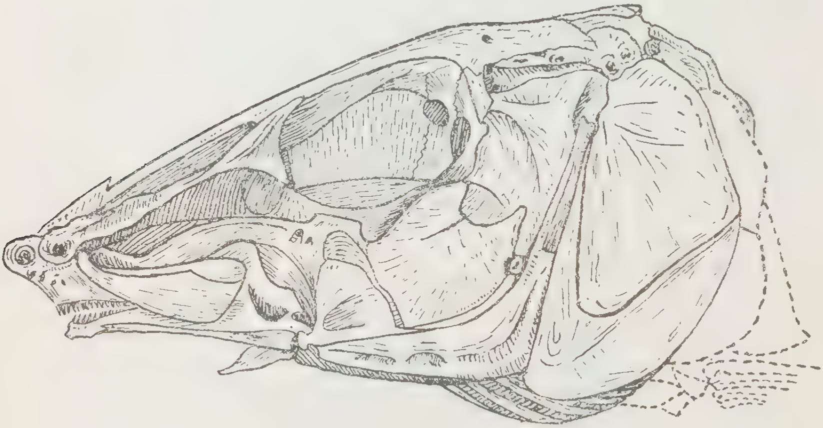

Fig. 125. *Albula vulpes* (L.). Skull seen from the left side. After GREGORY (1933), fig. 37 A on p. 145.

In *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*), however, which belongs to this group, conditions differ considerably, because there is a real rostrum, consequently the mouth is inferiorly placed and directed downward. Moreover the new upper jaw has a downward slope in connection with the fact that its prolongation runs dorsal of the quadratum-articulare joint (pp. 175, 416, fig. 66) (see my fig. 64).

f) The snout is short in a longitudinal direction but shows a downward prolongation and the quadratum-articulare joint lies far ventral. Then the lower edge of the new upper jaw may yet incline upwards, it may also be practically horizontal again, and it is also possible that it would slope downwards.

An upward inclined lower edge of the new upper jaw is found in a number of cases from several main types.

We find it in the following two forerunners of the first main type (jaws short, snout long): *Platax teira* (Forsk.) (fig. 151) (see my fig. 126) and *Chaetodipterus* (fig. 152); further in *Petrocephalus bane* (Lac.) (fig. 64) (see my fig. 88), which is derived from the first main type.

We also find it among the second main type (jaws long, snout long) in *Haemulon*, where the lower edge of the new upper jaw is only slightly tilted upwards and where the tip of the mouth is brought forward, and thus makes a more horizontal gape (p. 248, fig. 121) (see my fig. 127).

Among the cases from the fourth main type (jaws short, snout short) we find this condition f) with an upward sloping lower edge of the new upper jaw in *Iniistius*, where the information that the jaws are deep vertically, as far as it does concern the new upper jaw, must refer to the slope (p. 257, fig. 132) (see my fig. 128).

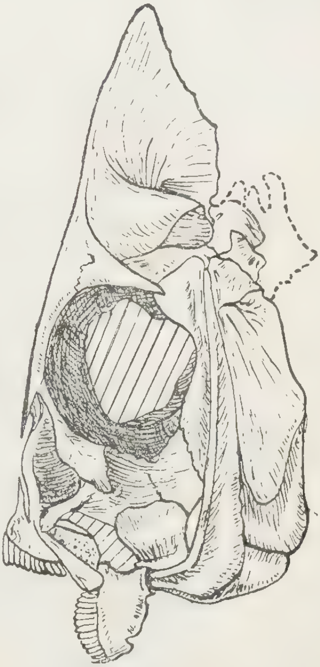
Fig. 126. *Platax teira* (Forsk.). Skull seen from the left side. After GREGORY (1933), fig. 151 on p. 275.

A practically horizontal lower edge of the new upper jaw is also found in representatives from different main types.

Among the second main type (jaws long, snout long) we find it in *Lachnolaimus maximus* (Walbaum), one of the Labridae of which it is said that it has a horizontal mouth due to the forward and downward elongation of the snout (p. 256, fig. 130) (see my fig. 129).

Among the representatives of the fourth main type (jaws short, snout short) we find this condition in *Periophthalmus* (fig. 228) (see my fig. 41).

Examples of the third possibility, *viz.* a downward sloping lower edge of the new upper jaw, are, as far as I know, not known.

In Reptilia the new upper jaw very often extends as far as below, or even behind the orbita. Exact data about this I did not find in the literature I consulted; special research in this direction would seem to be advisable. By virtue of its definition, the snout also in Reptilia, lies preorbital.

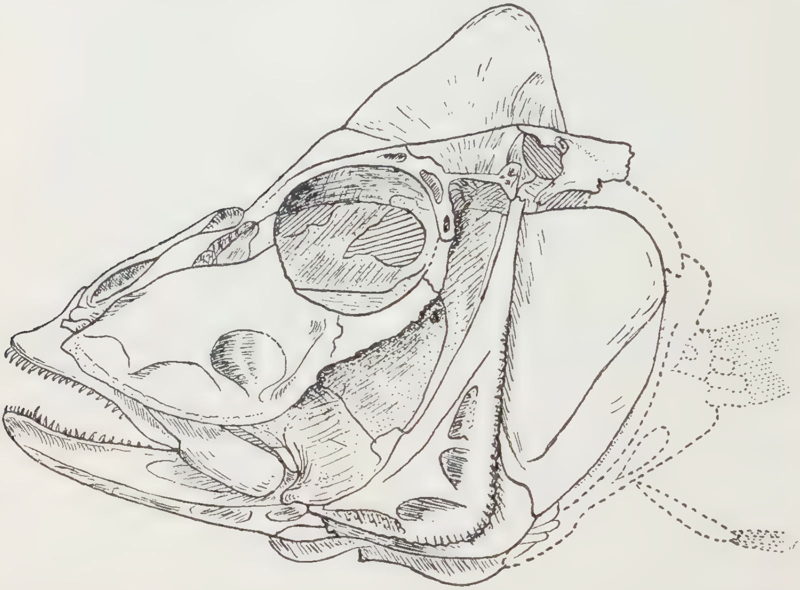

Fig. 127. *Haemulon.* Skull seen from the left side. After GREGORY (1933), fig. 121 on p. 247.

In Aves we notice a tendency for the upper bill to be pushed forward, in front of the eyes, the eyes separating the cerebral capsule from the upper bill (MARINELLI, 1936, pp. 809, 811).

The extension of the new upper jaw with regard to the orbita in Mammalia, is not mentioned in the literature consulted, either. Here, too, special research would be advisable. By virtue of its definition the snout of Mammalia lies preorbital as well.

The last point we want to discuss is the situation and the modification of the situation of the right and left half of the upper jaw of Heterosomata, where the mouth is twisted during development so as to face more on the upturned side of the body (GREGORY, 1933, p. 417).

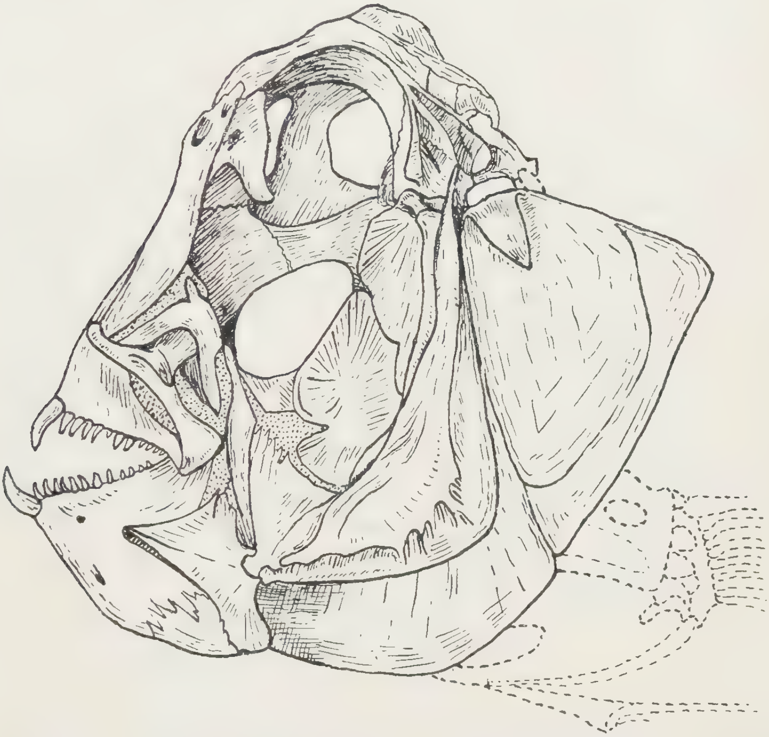

Fig. 128. *Iniistius*. Skull seen from the left side. After GREGORY (1933), fig. 132 on p. 258.

d. Homology and non-homology

In judging the differences in size and situation of upper jaw (upper bill), rostrum and snout, we must keep in mind that these formations are not homologous. We expressly pointed this out in the beginning of this paragraph.

Furthermore, the primary rostrum is not homologous with the secondary one.

Formations indicated by one certain name, are not quite the same, either. Thus the share which the different sorts of rostralia, lacrimalia and nasalia have in the formation of the secondary rostrum or snout in Teleostomi, may be entirely different. Therefore the snout, which is nothing but the preorbital part of the skull, is built up in different degrees by different elements (Holmgren & Stensiö, 1936, pp. 474ff). The share which the two elements of the new upper jaw have in its construction differs, too. Thus the snout of *Tylosurus* is principally formed by the praemaxillare (Gregory, 1933, p. 221). The snout of Loricata (Crocodilia) is principally formed by the maxillare; that of † Phytosauria by the praemaxillare, that of † Ichthyosauria by the strongly elongated praemaxillaria, nasalia and maxillaria (Versluys, 1936, pp. 788, 789, 797). In Aves the elongation of the upper bill is nearly entirely due to the praemaxillare, which, indeed, is the larger element; the maxillare has nearly completely been ousted from its original place and importance; the share of maxillare and praemaxillare in the formation of the lateral edge

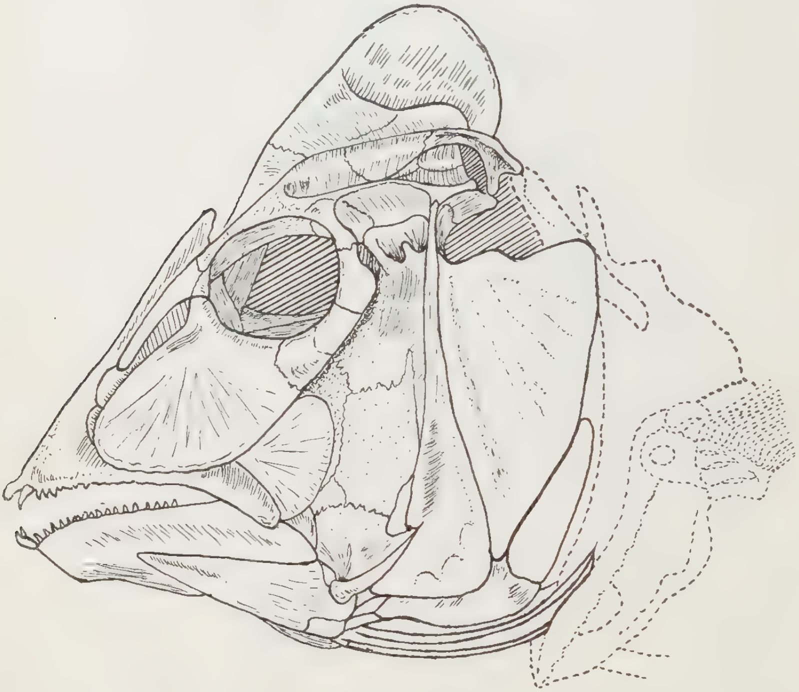

Fig. 129. *Lachnolaimus maximus* (Walbaum). Skull seen from the left side. After Gregory (1933), fig. 130 on p. 256.

of the upper bill is very changeable, the nasale often takes an important part in the structure of the upper bill, while, finally, a processus praenasalis occurs as the nucleus of the upper bill (STRESEMANN, 1927, p. 48; MARINELLI, 1936, pp. 809, 825/826).

6. LOWER JAW

a. Introduction

When the lower jaw is treated here as one single functional component of the skull, it must be borne in mind, that viewed according to the standard applied in an other part of this article, the lower jaw comprises some functional components. The lower jaw is the bearer of the dental plate, but also the place of attachment of the chewing-muscles and contains moreover a part of the jaw joint. With regard to the Pisces GREGORY (1933, p. 414, figs 284, 285) expresses it thus: that each half of the lower jaw forms a simple lever of the third class, pivoted on the quadrate bone by a hinge-like joint; the main tendons of the jaw muscles are inserted in front of the pivot and behind the teeth, through which the power is applied to the resistance. In connection with this the following information of MARINELLI, which he gives in passing (1929, p. 132), is important. According to his conception of the upper jaw with the system of zygomatic arches *etc.*, as a bridge-like construction is also applicable to the lower jaw, so that here, too, we must distinguish two piers and a carrying part.

In the following by lower jaw will be understood the skeletal bar running to left and to right from the rostral connection in the median plane to the jaw joint. So the following discussion will not include the gularia, one or more skeletal elements, which cover the bottom of the mouth cavity between the right and left half of the skeletal lower jaw in many lower Teleostomi and in a single group of Teleostei (HOLMGREN & STENSIÖ, 1936, pp. 362, 367, 397, 463, 496).

b. The size of the lower jaw

The size of the lower jaw is closely connected with that of the upper jaw. For the length taken up by the series of teeth, or by the teeth and back-teeth, is generally equal in upper and lower jaw. But caudal of this row of teeth or teeth and back-teeth there is, in the lower jaw, a toothless part to which the chewing-muscles attach themselves and which helps to form the jaw joint. Opposite this hindmost, toothless part of the lower jaw, which we should like to treat as one single functional component together with the toothbearing part, there is, however, no functioning upper jaw. In Elasmobranchii the back part of the palatoquadratum is, functionally, no upper jaw; in the higher Pisces the same is the case with skeletal elements which have originated from this back part of the palatoquadratum, or have come to be situated against it, while in Amphibia and Sauropsida the same is the case with the caudal part of the palatoquadratum and also with the jugal and the quadratojugal, connecting the back edge of the new upper jaw with the back part of the palatoquadratum. Finally, in Mammalia part of the zygomatic arch is situated opposite the toothless caudal part of the lower jaw. So we may conclude that no upper jaw is situated opposite the toothless caudal part of the lower jaw; the short toothless extreme edge of the maxillare hardly influences this conclusion. So we may conclude that the lower jaw is, in general, longer than the upper jaw, both absolutely and relatively.

In the above our starting-point has been the generally occurring condition that the lower jaw protrudes just as far as the upper jaw. But in some cases this is not so. In some cases the lower jaw protrudes farther than the upper jaw. Thus *e.g.* in *Rhynchops* the lower bill is 15-20 mm longer than the upper bill (Owen, 1866 II, pp. 147/148; Stresemann, 1929, p. 470; Böker, 1937, p. 69). In a number of Pisces, too, the lower jaw reaches farther rostralward than the upper jaw, though no measure is indicated. Thus, in *Belone*, the lower jaw reaches farther forward than the upper jaw, as is also the case in a more marked degree in species of the genus *Hemirhampus* (Böker, 1937, p. 24). From pictures in Gregory (1933) some data may also be derived on this point. In many pictures the skull has been drawn with open mouth; in such cases the lower jaw reaches farther to the left in the picture of skulls with an upward-sloping lower edge of the upper jaw. If we imagine the mouth closed, the foremost point of the lower jaw will, in most cases, not be situated past the perpendicular erected in the foremost point of the upper jaw on the lower edge of the upper jaw, so that in such cases the lower jaw does not actually reach farther forward than the upper jaw. Sometimes it is very difficult to decide this on the strength of the picture. We want to point out the picture of *Trichiurus lepturus* L. (figs 195, 291 D), where the lower jaw makes the impression of reaching farther forward than the upper jaw, but where we cannot make quite certain from the picture only. In my opinion the case is quite clear in *Roccus lineatus* (Bl.) (fig. 119) (see my fig. 19), *Echeneis* (fig. 199), and *Parachaenichthys georgianus* (Fischer) (fig. 239 C). The lower jaw protrudes to a lesser degree in *Auxis thazard* (Lac.) (fig. 190) and in *Exocoetus evolans* L. (*Halocypselus evolans*) (fig. 101) (see my fig. 27).

The reverse condition also occurs, *viz.* that the upper jaw reaches farther forward than the lower jaw. When this is the case, it is of course not possible to say beforehand whether the lower jaw is even now longer than the upper jaw. As a rule this will, however, be the case because the length of the extension of the upper jaw beyond the lower jaw is slight in proportion to the length of the toothless part of the lower jaw, opposite which no real upper jaw is situated. Judging from GREGORY's pictures (1933) it occurs in comparatively many Pisces that the upper jaw protrudes in front of the lower jaw. It is so pictured for *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*), about which GREGORY (1933, p. 176, fig. 66) (see my fig. 64) informs us that the lower jaw is much longer than the maxilla. In this connection we want to point out the following pictures in GREGORY (1933): † *Cheirolepis trailli* Agassiz (fig. 12 A) (see my fig. 95), *Galaxias attenuatus* (Jenyns) (fig. 50), *Gonostoma elongatum* Gthr (fig. 53), *Brycon dentex* Gthr (fig. 70), *Plecostomus commersonii* (Val.) (fig. 80), *Anableps tetrophthalmus* Bl. (fig. 98) (see my fig. 40), *Prionotus* (fig. 218), *Trigla hirundo* Bl. (fig. 219), *Dactylopterus* (*Cephalacanthus*) (fig. 222), *Mastacembelus* (fig. 233), *Percis nebulosa* Q. & G. (fig. 237 B), *Callionymus* (fig. 242), *Blennius* (fig. 252), *Melanonus* (fig. 260) and *Lasiognathus* (fig. 275).

Also in Aves we meet with the phenomenon that the upper bill reaches farther forward than the lower one. This is the case, to a high degree, in *Heterorhynchus* (STRESEMANN, 1929, pp. 442/443). Further we may here mention numberless cases where an upper bill curves rostrally round a lower bill which reaches less far forward (see my figs 34, 56). This occurs amongst others in birds of prey, where the claw has become a prehensile organ which by compensatory relief ("kompensatorische Entlastung") has taken over part of the function of the bill (GROEBBELS, 1932, p. 395).

I do not know whether the fact that, in † Pyrotheria, the lower jaw clearly shows the influence of the tusks (STADTMÜLLER, 1936,

p. 979), points to a difference in the situation of the front edges of the upper bill and the lower one.

The absolute size of the lower jaw

Direct data about the absolute size of the lower jaw, are not at my disposal.

What has been said about the absolute size of the upper jaw may be referred to here with the addition that the absolute size of the lower jaw is even more considerable. An exception to this may only be formed by certain cases where the lower jaw protrudes less far than the upper one.

The relative size of the lower jaw

As regards the relative size of the lower jaw, we may also refer to the general points of view and to the exact data that have been given in discussing the upper jaw.

For the lower jaw it also holds good that there is a connection between the size of the body and that of the lower jaw, and that this connection is influenced by many factors, connected with the seizing of the food, and with the mastering, chopping up and consumption of the food, so in both cases connected with the character of the food, and in the third place connected with accessory factors which we mentioned when discussing the upper jaw (function of the jaw in sexual play, in climbing *etc.*).

Like in the discussion of the upper jaw we will here successively discuss length, breadth and height of the lower jaw.

We will limit ourselves to definite data on these three dimensions of the lower jaw.

In general the relative length of the lower jaw runs parallel with that of the upper jaw. It is, however, unknown to me what influence the difference between the absolute length of the upper jaw and that of the lower jaw has on the relative length of the lower jaw. This is connected with the proportion between the length of the tooth-bearing and the toothless part of the lower jaw.

This proportion between the tooth-bearing and the toothless part of the lower jaw is, roughly, the same as the proportion between the length of the dentale and the part situated caudal of it. This proportion is rather varying in Pisces. In *Electrophorus* the dentale is large, but, according to the picture, the caudal part of the lower jaw is very short (GREGORY, 1933, p. 187, fig.

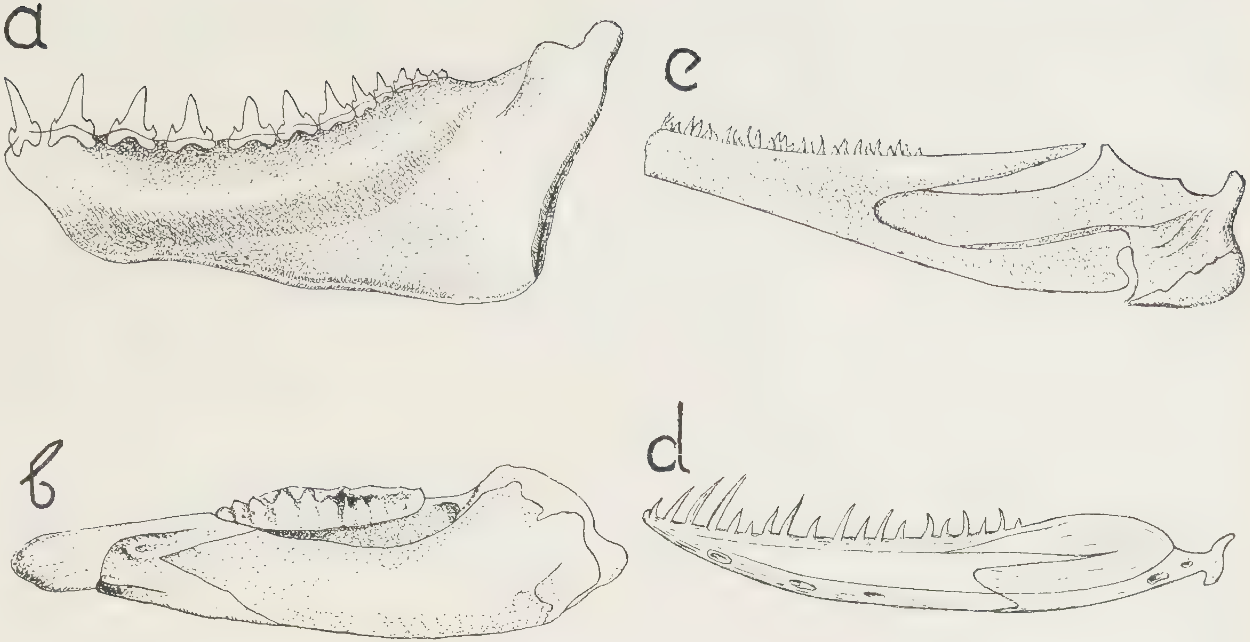

Fig. 130. Left half of lower jaw of Pisces seen from the left side. All lower jaws are drawn to an equal length of the distance from the foremost point of the lower jaw to the middle of the articular joint. *a*. *Isurus nasus* (Bonnaterre) (*Lamna cornubica* (Gmelin)). Right lower jaw seen from the right side inverted. After Abel (1919), fig. 81 on p. 122. *b*. *Dipterus platycephalus* Ag. After Holmgren and Stensiö (1936), IV, fig. 281 on p. 367. *c*. *Gadus morrhua* L. After Bütschli (1910), fig. 142 A on p. 251. *d*. *Chiasmodon*. After Gregory (1933), fig. 137 on p. 263.

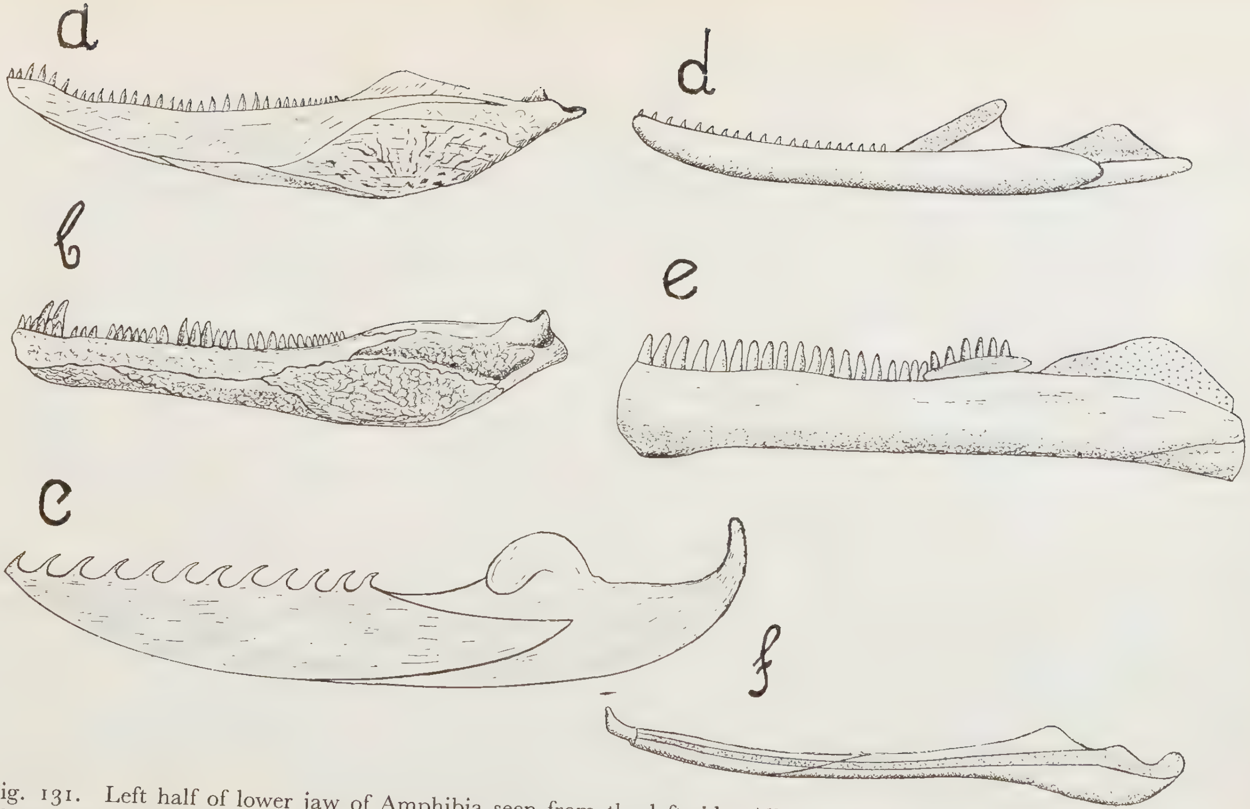

Fig. 131. Left half of lower jaw of Amphibia seen from the left side. All lower jaws are drawn to an equal length of the distance from the foremost point of the lower jaw to the middle of the articular joint. *a. Eryops megacephalus* Cope. 0.17×. After Abel (1919), fig. 190 B on p. 245. *b. Trimerorhachis.* Right lower jaw seen from the right side inverted. After Versluys (1924), II, fig. 594 B on p. 317. *c. Ichthyophis glutinosus* (L.). After Bütschli (1910), fig. 149 on p. 264. *d. Cryptobranchus alleganiensis* (Daud.) (*Menopoma alleghaniense*). After Bütschli (1910), fig. 147 *c* on p. 261. *e. Necturus maculosus* (Raf.) (*Necturus maculatus*). Right lower jaw seen from the right side inverted. After Gaupp (1913), fig. 39 on p. 84. *f. Rana temporaria* L. (*Rana fusca*). After Bütschli (1910), fig. 148 *c* on p. 263.

73 B). In *Percopsis guttatus* Ag. the small lower jaw contains a minute dentale but a relatively large articulare (p. 232), also in *Capros aper* (L.) the dentale is very short, whereas the angulare-articulare is elongate (p. 272, fig. 149 A). In *Cheilodactylus* the dentale is extremely short, the part of the lower jaw situated caudal of it is short as well (p. 260, fig. 136); in *Mormyrops* the dentale is rather short and the rest of the lower jaw, situated behind it is very short too (p. 171, fig. 62 A). In Xenopterygii the dentale is also short while in the picture of *Gobiesox*, which is referred to, the part of the lower jaw situated behind it, is not very long either (p. 371, fig. 249). We refer also to the following figures in this article: *Salmo* (see my fig. 18); *Esox masquinongy* Mitchill (see my fig. 30); *Anableps tetrophthalmus* Bl. (see my fig. 40); *Periophthalmus* (see my fig. 41); *Coila nasus* Temm. Schl. (see my fig. 77); *Brama rayi* (Bl.) (see my fig. 83); *Gastrostomus* (see my fig. 87); *Archosargus probatocephalus* (Walbaum) (see my fig. 89); *Tylosurus marinus* (Walbaum) (see my fig. 94); *Osteoglossum* (see my fig. 116); *Lycodontis funebris* (Ranzani) (see my fig. 119); *Chauliodus sloanei* Bl. Schn. (see my fig. 122); *Dipterus platycephalus* Ag. (see my fig. 130 *b*) and *Chiasmodon* (see my fig. 130 *d*).

When indirectly determining the length of the lower jaw from other data, we must bear in mind that the length of the mouth is no direct indication of the length of the lower jaw.

Thus GREGORY mentions (1933) that in *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*) only the front part of the lower jaw enters into the gape (p. 176, fig. 66) (see my fig. 64) and that, considering the very long lower jaw in *Stylophorus chordatus* Shaw one would expect to find a huge mouth, but on the contrary, the mouth is quite small (p. 299).

When determining the length of the lower jaw of Pisces, we must, furthermore, also pay attention to the phenomenon that in some species the dentary teeth are fused into a lower beak, through which a forward prolongation of the foremost point of the lower jaw originates (GREGORY, 1933, pp. 251, 257) (see my figs 78, 121).

Let us now pass on to informations about the relative length of the lower jaw in literature.

Among Pisces the lower jaw of *Tylosurus* is excessively elongated (GREGORY, 1933, p. 221, fig. 99) (see my fig. 94); in *Stylophorus chordatus* Shaw the lower jaw is very long (p. 299, fig. 176); in *Esox masquinongy* Mitchill it is very large (p. 214, fig. 95) (see my

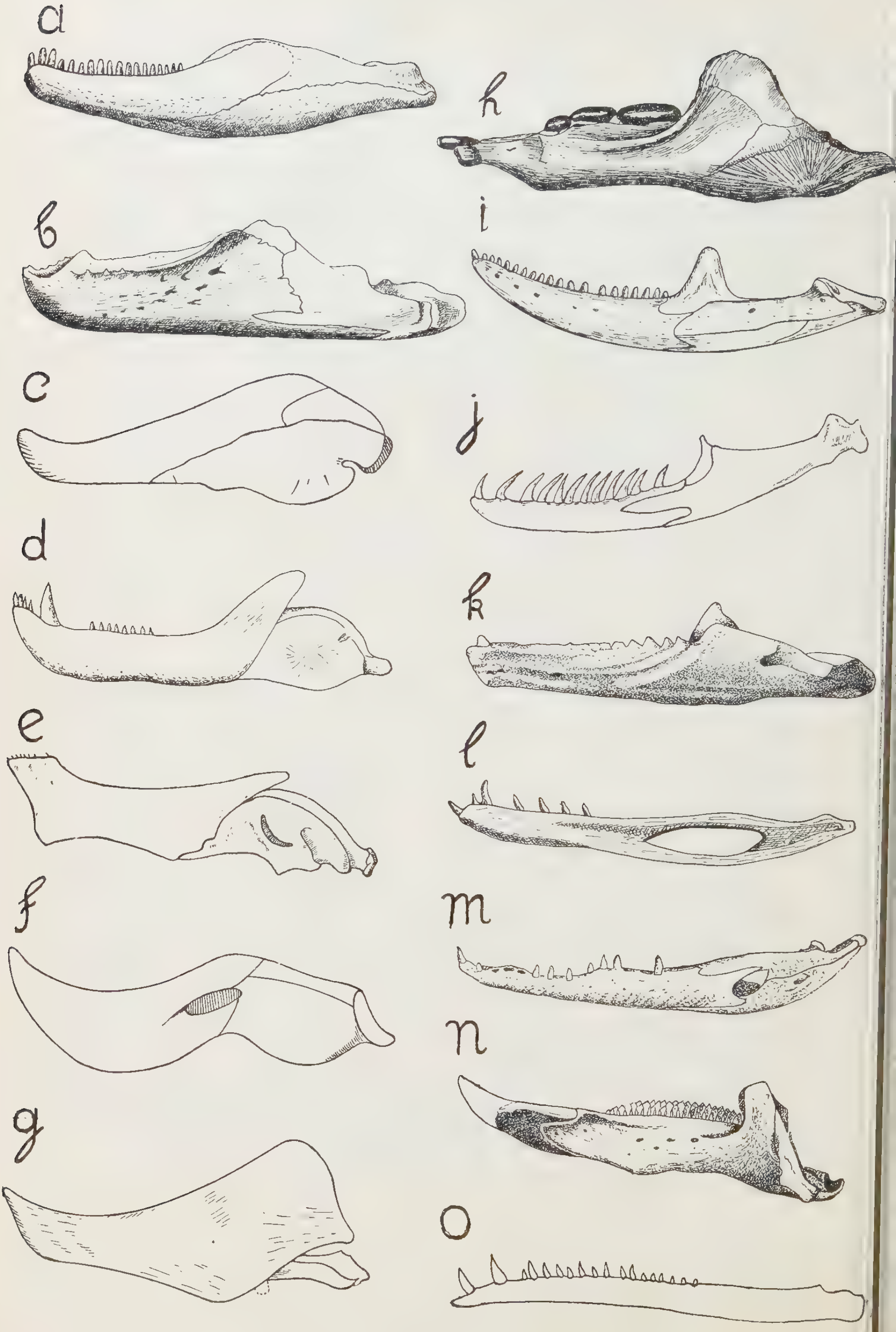
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fig. 30) while the lower jaw in *Chaetodon* is long (p. 279, fig. 155). According to Böker (1937, p. 24) the lower jaw in *Belone* is long. We also refer to the following figures in my article: *Salmo* (see my fig. 18); *Chlamydoselachus anguineus* Garman (see my fig. 62); *Engraulis encrasicholus* (L.) (see my fig. 76); *Coila nasus* Temm. Schl. (see my fig. 77); *Gastrostomus* (see my fig. 87); † *Cheirolepis trailli* Agassiz (see my fig. 95); *Osteoglossum* (see my fig. 116); *Lycodontis funebris* (Ranzani) (see my fig. 119) and *Chauliodus sloanei* Bl. Schn. (see my fig. 122).

In *Lampris* the lower jaw is much shorter than in the more primitive *Velifer* (Gregory, 1933, pp. 298/299, figs 173, 174). Also in *Percopsis guttatus* Ag. the lower jaw is small (p. 232). In *Characodon luitpoldii* Steind. ("*Goodea atripinnis*") the lower jaw is extremely small, in *Anableps tetrophthalmus* Bl. the lower jaw is minute (p. 220, fig. 98) (see my fig. 40). *Chaetodipterus* is aberrantly specialized in the shortening of the lower jaw; it approaches the Scaridae in the marked shortening of the dentale and articulare which brings the biting surface near the fulcrum and gives it great power (Gregory, 1933, p. 278). According to

Fig. 132. Left half of lower jaw of Reptilia seen from the left side. All lower jaws are drawn to an equal length of the distance from the foremost point of the lower jaw to the middle of the articular joint. *a. Labidosaurus hamatus* Cope. Right lower jaw seen from the right side inverted. After Versluys (1924), II, fig. 612 b on p. 341. *b. Chelonia mydas* (L.) (*Chelone midas*). After Schimkewitsch (1910), fig. 128 a on p. 116. *c. Dimetrodon.* Right lower jaw seen from the right side inverted. After Versluys (1924), II, fig. 631 a on p. 367. *d. Scylacosaurus sclateri* Broom. After E. Gaupp (1913), fig. 142 on p. 273. *e. Leptotrachelus eupachygnathus* Watson (*Scymnosuchus*). Right lower jaw seen from the right side inverted. After Versluys (1924), II, fig. 631 b on p. 367. *f. Oudenodon* (*Udenodon*). After Versluys (1924), II, fig. 607 c on p. 333. *g. Cynognathus.* Right lower jaw seen from the right side inverted. After Versluys (1924), II, fig. 631 d on p. 367. *h. Placodus gigas* Ag. 0.33×. After K. A. v. Zittel (1923), fig. 405 e on p. 290. *i. Lacerta agilis* L. Right lower jaw seen from the right side inverted. After Versluys (1924), II, fig. 613 b on p. 341. *j. Python.* 0.57×. Collection Zool. Lab. Leiden. Original drawing by C. L. van Helden. *k. Sphenodon punctatus* Gray. 1.08×. After Kükenthal (1931), VII, 1. H., fig. 42 a on p. 39. *l. Ornithosuchus Woodwardi* E. T. Newton. Right lower jaw seen from the right side inverted. 0.52×. After Abel (1919), fig. 416 on p. 526. *m. Crocodylus vulgaris* Cuv. (*Crocodilus niloticus* Laurenti). Right lower jaw seen from the right side inverted. After E. Gaupp (1913), fig. 53 on p. 95. *n. Triceratops serratus* Marsh. 0.07×. After Stromer von Reichenbach (1912), fig. 90 a on p. 89. *o. Campylognathus.* 0.49×. After Williston (1925), fig. 71 b on p. 88.

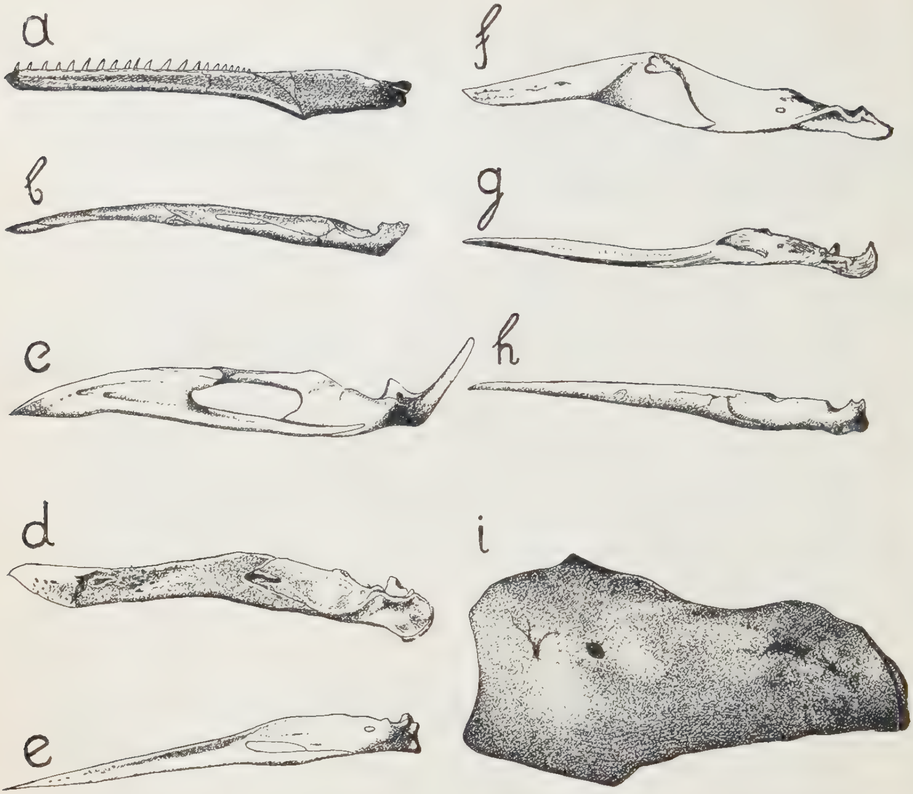

Fig. 133. Left half of lower jaw of Aves seen from the left side. All lower jaws are drawn to an equal length of the distance from the foremost point of the lower jaw to the middle of the articular joint. *a. Ichthyornis dispar* Marsh. 0.8×. After K. A. v. Zittel (1923), fig. 501 a on p. 395. *b. Tinamus* sp. After Marinelli (1936), IV, fig. 627 a on p. 818. *c. Tetrao urogallus* L. After Marinelli (1936), IV, fig. 629 b on p. 823. *d. Raphus cucullatus* (L.) (*Didus ineptus* L.). Right lower jaw seen from the right side inverted. 0.29×. After H. E. Strickland & A. G. Melville (1848), Plate VIII. *e. Anthropoides virgo* (L.). After Marinelli (1936), IV, fig. 627 b on p. 818. *f. Eudyptes sclateri* Buller (*Catarrhactes sclateri*). After Marinelli (1936), IV, fig. 629 a on p. 823. *g. Anas* sp. After R. Wiedersheim (1902), fig. 87 c on p. 117. *h. Sula* sp. After Marinelli (1936), IV, fig. 627 c on p. 818. *i. Ara macao* (L.). After Marinelli (1936), IV, fig. 630 a on p. 823.

Böker (1937, pp. 58/59) the lower jaw of *Serrasalmo* is extremely short. Among the Selachii the lower jaw of *Scymnorhinus* (*Scymnus*), which is the most strongly developed among Selachii, is very short

(Holmgren & Stensiö, 1936, p. 319). We also refer to the following figures in this paper: *Balistes carolinensis* Gmel. (see my fig. 43); *Squalus acanthias* L. (see my fig. 61); *Gnathonemus curvirostris* Blgr. (see my fig. 66); *Ogcocephalus vespertilio* (L.) (see my fig. 67); *Pseudoscarus guacamaia* (Cuv.) (see my fig. 78); *Eigenmannia macrops* (Blgr.) (see my fig. 80); *Opisthoproctus* (see my fig. 84); *Alutera scripta* (Osbeck) (see my fig. 91); *Fistularia* sp. (see my fig. 93); *Zanclus cornutus* (L.) (see my fig. 117); *Lactophrys tricornis* (L.) (see my fig. 118) and *Platax teira* (Forsk.) (see my fig. 126).

Among Amphibia the lower jaw is relatively very long in *Ichthyophis* (see my figs 31, 96) [1]).

Among Reptilia the lower jaw is relatively very long in the following cases figured in this article: *Ornithodesmus* (see my fig. 44); *Stenopterygius* (see my fig. 103); *Micrurus* (see my fig. 104) and *Bitis* (see my fig. 105).

Among Aves the lower jaw is relatively very long in all cases figured in this article, *viz.* in *Caprimulgus* (see my fig. 33); *Ramphastos* (see my fig. 69); *Numenius* (see my fig. 98) and *Pelecanus* (see my fig. 106).

Among Mammalia the relative length of the lower jaw shows much variation. It is relatively very long *e.g.* in *Zaglossus* (see my fig. 107 *a*), it is relatively very short in Man. As regards Cetacea we refer to the differences between *Mesoplodon* (see my fig. 70 *a*) and *Kogia* (see my fig. 110 *a*).

As regards Proboscidea we will point out the considerable difference in the relative length of the lower jaw in *Elephas* and in † *Mastodon*, but also between the different species of the genus † *Mastodon* mutually (Böker, 1937, p. 113) (see my fig. 134 *aa*).

As regards the relative breadth of the lower jaw we may also refer to the information given in the discussion of the upper jaw. The data compiled there on the breadth of the opening of the mouth, of the mouth cavity and the distance between the right and the left jaw joint, allow of analogous conclusions with regard to the lower jaw. So we shall limit ourselves to some information bearing on the lower jaw more especially.

Among Pisces a relatively broad lower jaw is figured in this

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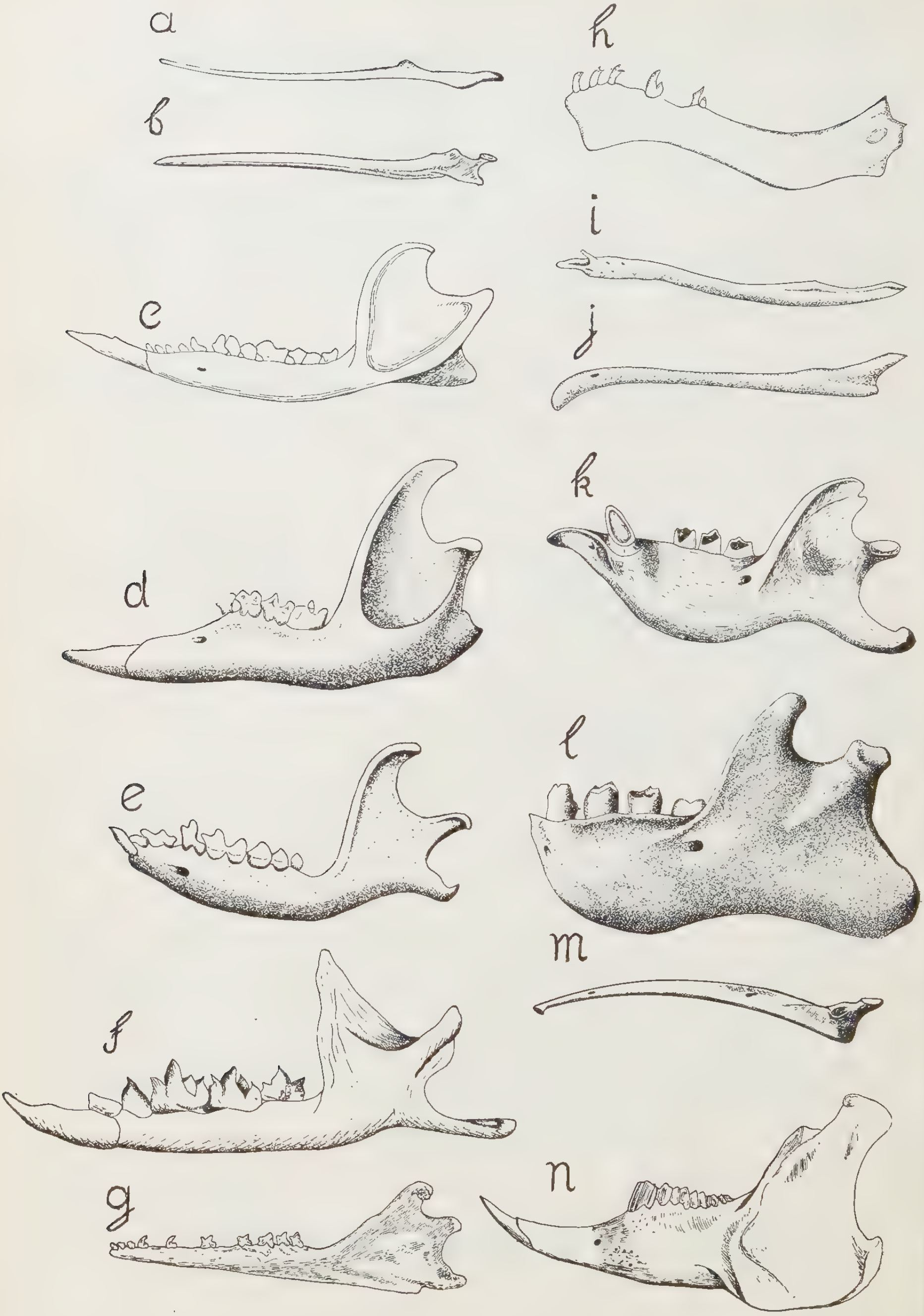
[1]) For the lower jaw of † Stegocephala, see: T. Nilsson (1944), K. Svensk. Vetensk. Handl. **21**, pp. 1–70. (Postwar addition in the manuscript)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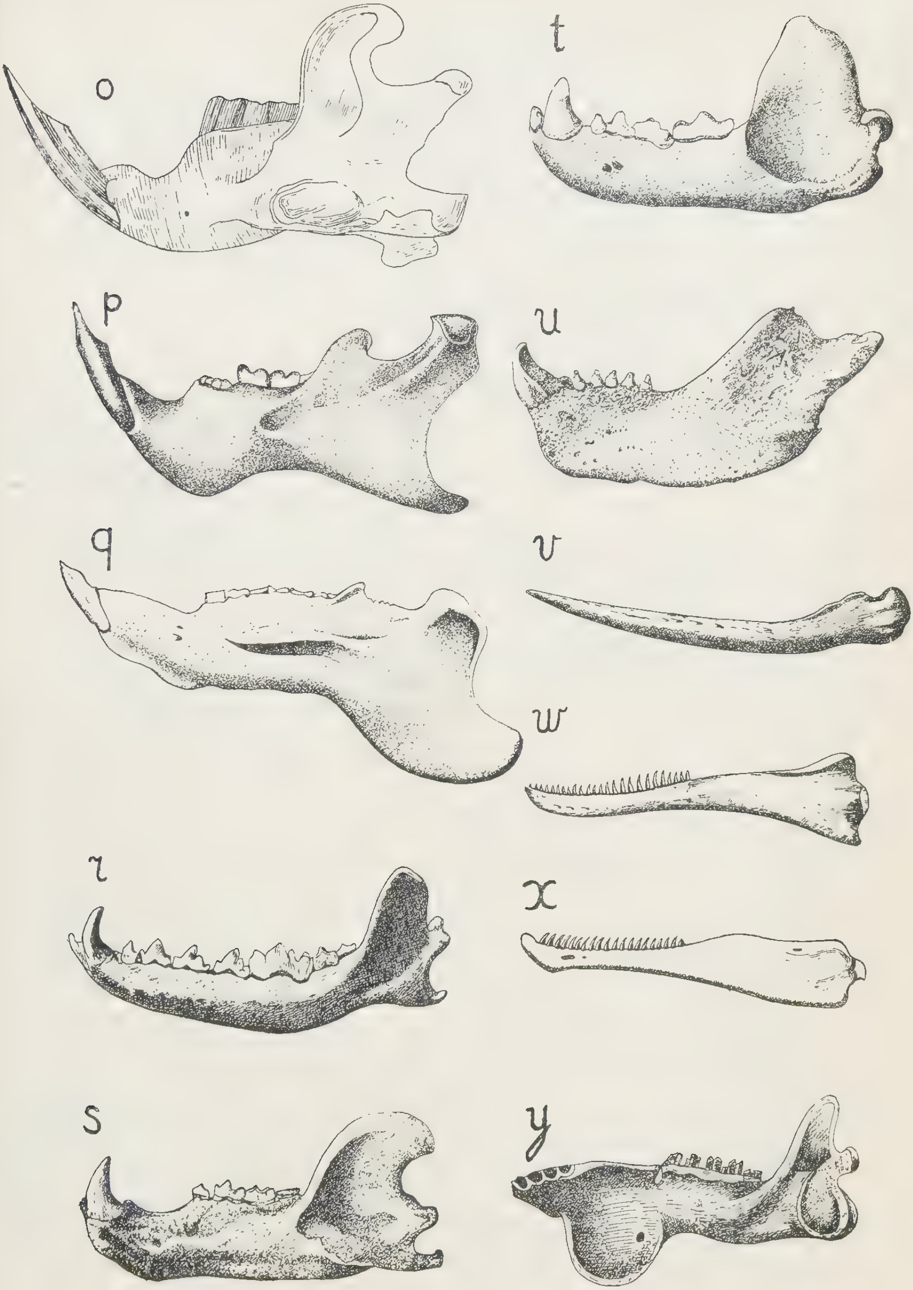
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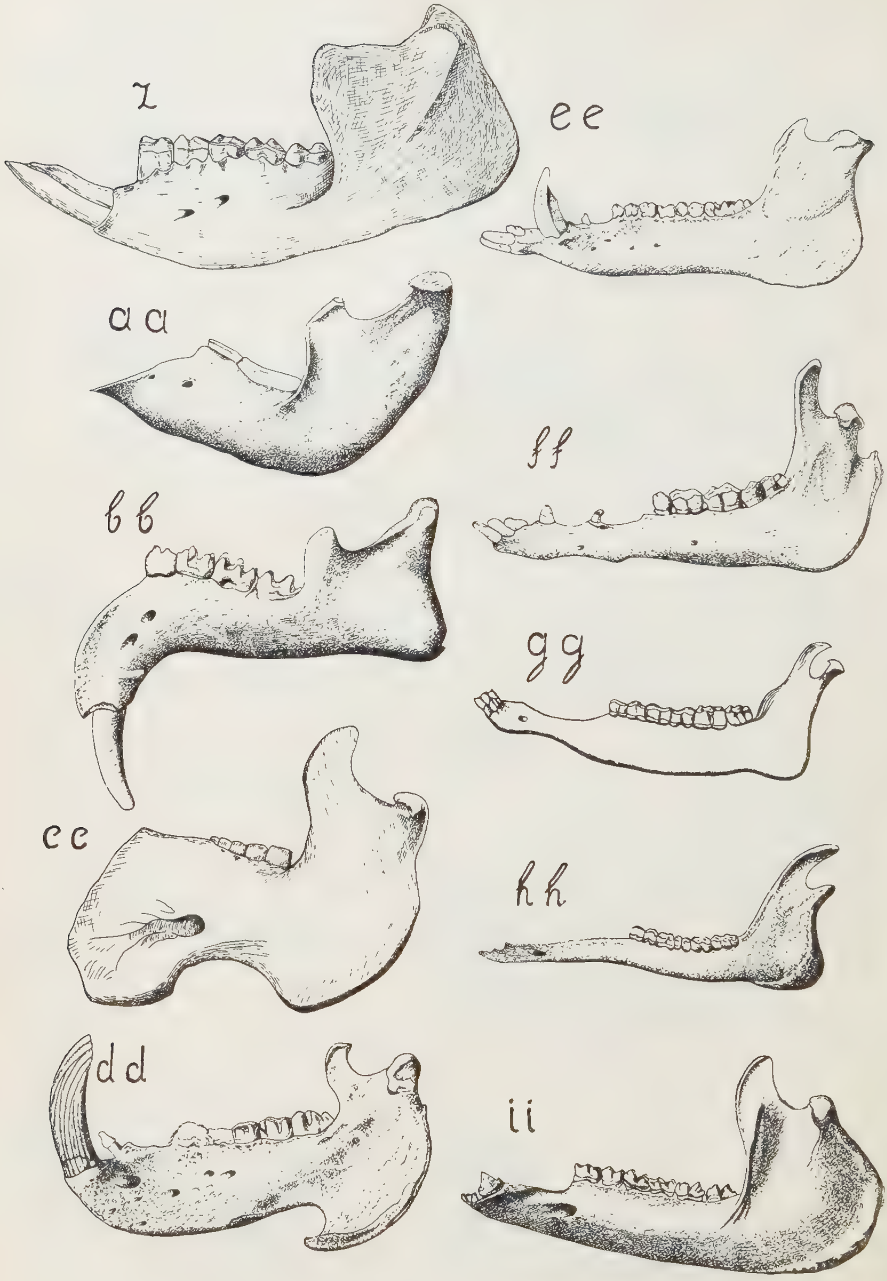
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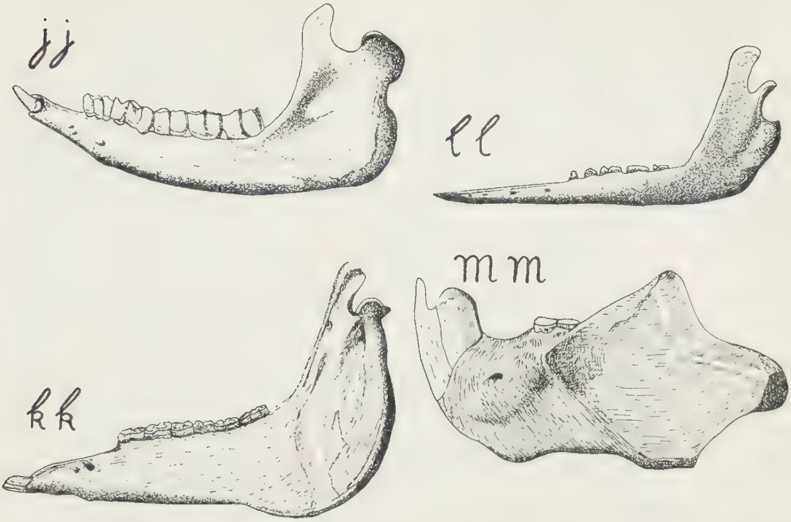

Fig. 134. Left half of lower jaw of Mammalia seen from the left side. All lower jaws are drawn to an equal length of the distance from the foremost point of the lower jaw to the middle of the articular joint. *a. Tachyglossus aculeatus* (Shaw) (*Echidna hystrix*). After Bütschli (1910), fig. 177 on p. 306. *b. Zaglossus bruynii* (Peters & Doria) (*Proechidna Bruyni*). Right lower jaw seen from the right side inverted. After M. Weber (1904), fig. 55 on p. 71. *c. Caenolestes.* After M. Weber (1928), II, fig. 38 on p. 75. *d. Halmaturus.* 0.47× . After M. Weber (1904), fig. 55 on p. 71. *e. Erinaceus europaeus* L. After M. Weber (1904), fig. 55 on p. 71. *f. Sylvisorex johnstoni* (Dobson) (*Myosorex johnstoni*). Right lower jaw seen from the right side inverted. 6.8× . After M. Weber (1928), II, fig. 58 on p. 98. *g. Hemicentetes semispinosus* Cuvier. 1.57× . After Flower & Lydekker (1891), fig. 295 on p. 638. *h. Pipistrellus abramus* (Temm.). Right lower jaw seen from the right side inverted. After M. Weber (1928), II, fig. 88 on p. 143. *i. Manis javanica* Desm. After M. Weber (1928), II, fig. 99 a on p. 176. *j. Tamandua tetradactyla* (L.). After M. Weber (1928), II, fig. 99 b on p. 176. *k. Eucholoeops externus* Amegh. Right lower jaw seen from the right side inverted. 0.25× . After O. Abel (1919), fig. 581 on p. 776. *l. Bradypus tridactylus* L. Right lower jaw seen from the right side inverted. After Ducrotay de Blainville (1839–1864), Atlas Tome IV, G. *Bradypus* Pl. III. *m. Myrmecophaga tridactyla* L. (*Myrmecophaga jubata* L.). After Bütschli (1910), fig. 177 on p. 306. *n. Lepus europaeus* Pallas (*Lepus timidus* L.). After Flower & Lydekker (1891), fig. 216 on p. 492. *o. Aplodontia leporina* Rich. Right lower jaw seen from the right side inverted. After G. v. Hayeck (1893), IV, fig. 3888 on p. 544. *p. Coendou affinis* Brandt (*Cercolabes affinis*). 1.2× . After E. Gaupp (1913), fig. 73 on p. 120. *q. Hydrochoerus capybara* Erxl. 0.35× . After M. Weber (1904), fig. 55 on p. 71. *r. Vulpes vulpes* (L.) (*Canis vulpes* (L.)). After Schimkewitsch (1910), fig. 142 a on p. 130. *s. Thalarctos maritimus* Phipps (*Ursus maritimus* Desm.).♀. Right lower jaw seen from the right side inverted. 0.23× . After Ducrotay de Blainville (1839–1864), Atlas Tome II, G. *Ursus* Pl. V. *t. Mellivora ratel* Sparrm. (*Mellivora capensis* Shreb.). Right lower jaw seen from the right side

inverted. After Ducrotay de Blainville (1839–1864), Atlas Tome II, G. *Mustela* Pl. VI. *u. Mirounga leonina* (L.) (*Phoca leonina*). Right lower jaw seen from the right side inverted. 0.13×. After Ducrotay de Blainville (1839–1864), Atlas Tome II, G. *Phoca* Pl. V. *v. Balaena japonica* Lacépède. After Schimkewitsch (1910), fig. 145 on p. 133. *w. Delphinus* sp. After Schimkewitsch (1910), fig. 144 on p. 132. *x. Tursiops truncatus* (Mont) (*Delphinus tursio*). After Bütschli (1910), fig. 177 on p. 306. *y. Uintatherium mirabile* (Marsh) (*Dinoceras mirabile*). After G. v. Hayeck (1893), IV, fig. 3730 on p. 486. *z. Pyrotherium Sorondoi* Amegh. 0.19×. After M. Weber (1904), fig. 516 on p. 726. *aa. Loxodonta africana* (Blumenbach) (*Elephas africanus* L.). ♀. Right lower jaw seen from the right side inverted. 0.08×. After Ducrotay de Blainville (1839–1864), Atlas Tome III, G. *Elephas* Pl. III. *bb. Deinotherium giganteum* Kaup. Right lower jaw seen from the right side inverted. 0.07×. After Ducrotay de Blainville (1839–1864), Atlas Tome III, G. *Dinotherium* Pl. I. *cc. Dugong dugong* (Müller) (*Halicore dugong* Erxleb.). ♂. Right lower jaw seen from the right side inverted. After M. Weber (1928), II, fig. 312 on p. 482. *dd. Hippopotamus amphibius* L. ♂. Right lower jaw seen from the right side inverted. 0.08×. After Ducrotay de Blainville (1839–1864), Atlas Tome IV, G. *Hippopotamus* Pl. II. *ee. Sus scrofa* L. ferus. ♂. Right lower jaw seen from the right side inverted. 0.15×. After Ducrotay de Blainville (1839–1864), Atlas Tome IV, G. *Sus* Pl. IV. *ff. Camelus dromedarius* L. Right lower jaw seen from the right side inverted. 0.13×. After Ducrotay de Blainville (1839–1864), Atlas Tome IV, G. *Camelus* Pl. III. *gg. Cervus elaphus* L. After Bütschli (1910), fig. 177 on p. 306. *hh. Giraffa reticulata* de Winton (*Camelopardalis giraffa* Shreb.). ♂. Right lower jaw seen from the right side inverted. 0.09×. After Ducrotay de Blainville (1839–1864), Atlas Tome IV, G. *Camelopardalis* Pl. II. *ii. Tapirus indicus* Desm. Right lower jaw seen from the right side inverted. After Ducrotay de Blainville (1839–1864), Atlas Tome IV, G. *Tapirus* Pl. II. *jj. Dicerorhinus sumatrensis* (Fischer) (*Rhinoceros sumatrensis* Cuvier). ♀. Right lower jaw seen from the right side inverted. 0.06×. After Ducrotay de Blainville (1839–1864), Atlas Tome III, G. *Rhinoceros* Pl. II. *kk. Equus caballus* L. Right lower jaw seen from the right side inverted. 0.1×. After Ducrotay de Blainville (1839–1864), Atlas Tome III, G. *Equus* Pl. II. *ll. Orycteropus capensis* Gm. 0.24×. After M. Weber (1904), fig. 55 on p. 71. *mm. Daubentonia madagascariensis* (Gmel.) (*Chiromys madagascariensis*). 0.81×. After M. Weber (1928), II, fig. 521 on p. 738.

article in the following cases: *Astroscopus* (see my fig. 50) and *Myoxocephalus* (see my fig. 92).

Among Reptilia there is sometimes a distinct difference in the distance between the outer surfaces of the right and left lower jaw in the rostral part and in the caudal part of the lower jaw, owing to the fact that the two halves of the lower jaw do not diverge already at the rostral point of the lower jaw (see my fig. 135).

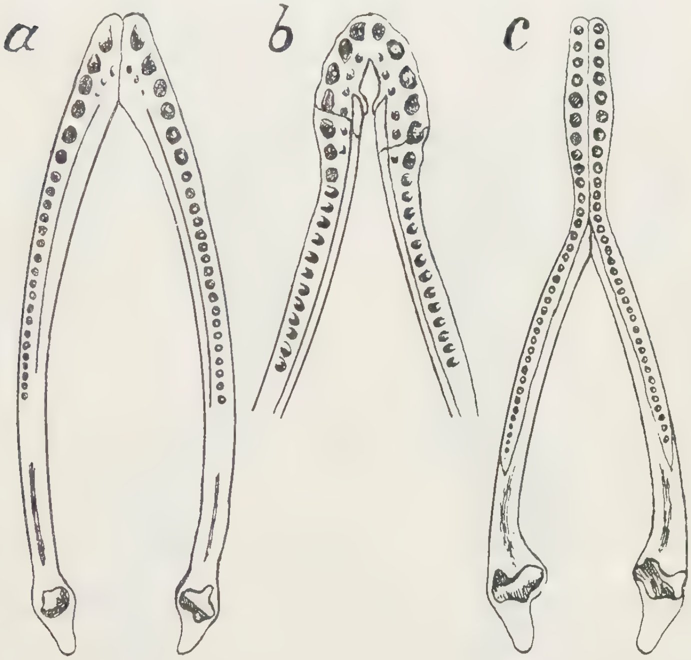

Fig. 135. Lower jaws of Reptilia seen from above. *a. Plesiosaurus dolichodeirus* Conyb. 0.24×. *b. Thaumatosaurus indicus* Lyd. 0.14×. *c. Peloneustes philarchus* Seeley. 0.12×. After O. ABEL (1919), fig. 391 on p. 497.

According to BÖKER (1937, p. 69) the lower jaw of *Rynchops* is said to be as narrow as a knife.

Among Mammalia the two halves of the lower jaw diverge from the rostral point where the joined lower jaws are narrow. There may occur, however, local widening of the lower jaw in a lateral direction (see my figs 136, 137). The widening may also occur in a medial direction so that even no open space at all is left between left and right half of the lower jaw in its rostral part, as is the case in *Halicore* (see my fig. 138). In a number of cases the rostral part of the joined lower jaws is not narrow; sometimes it is as broad as the more caudal part of the lower jaw (see my fig. 139). In the phylogeny of Equidae, the back part of the lower jaw, according to MARINELLI (1933, pp. 217, 218), is alleged to have become relatively broader, thus affording room to the thickening by contraction of the more strongly developing musculus pterygoideus, while at the same time the tubes in the throat were protected against being compressed. The rostral displacement of the jaw joint also has influenced this, because this displacement influences anything situated between the most caudal parts of the

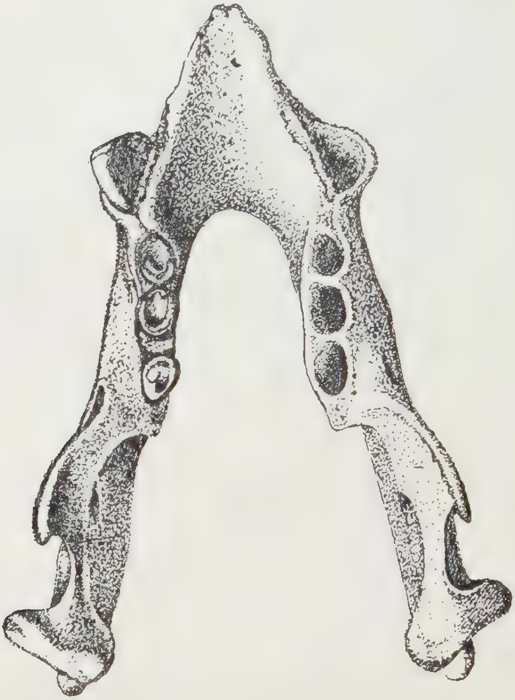

Fig. 136. *Choloepus didactylus* (L.) (*Bradypus didactylus*). Lower jaw seen from above. After DUCROTAY DE BLAINVILLE (1839–1864), Atlas Tome IV, G. *Bradypus* Pl. III.

lower jaw-halves. All this is more considerable in bigger species than in smaller ones, according to MARINELLI.

In some cases the breadth of the lower jaw may be altered, *viz.* when the two halves of the lower jaw may move as a result of the very loose connection in the symphysis mandibulae.

Thus, in *Gastrostomus* the rami mandibulares are loosely united at the symphysis and connected by a broad distensible membrane (GREGORY, 1933, p. 213).

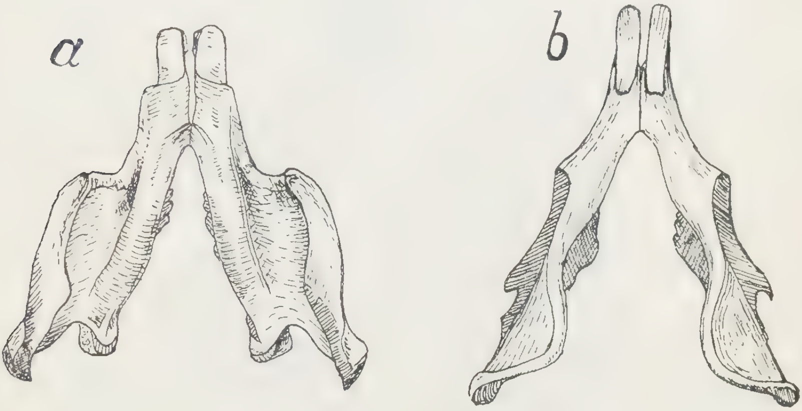

Fig. 137. Lower jaws of Rodentia seen from above. *a. Bathyergus suillus* (Schreb.) (*Bathyergus maritimus*). After M. WEBER (1928), II, fig. 160 on p. 246. *b. Marmota marmota* (L.). After M. WEBER (1928), II, fig. 161 on p. 246.

In Serpentes, too, we find a very distensible symphysis of the lower jaw (BÖKER, 1937, p. 140) (see my figs 104, 105).

As regards the height of the lower jaw, we shall treat the average height apart from the height of a local heightening of a processus on the lower jaw.

As regards the height of the lower jaw in general, this runs, as a rule, parallel with that of the upper jaw, because the height is the expression of the more or less strong structure of the lower jaw and the upper one. We are taught that this is not always the case in Ogcocephalidae where the lower jaw is delicate whereas the arcus palatoquadratus is unusually massive, apparently a secondary enlargement to support the massive neurocranium

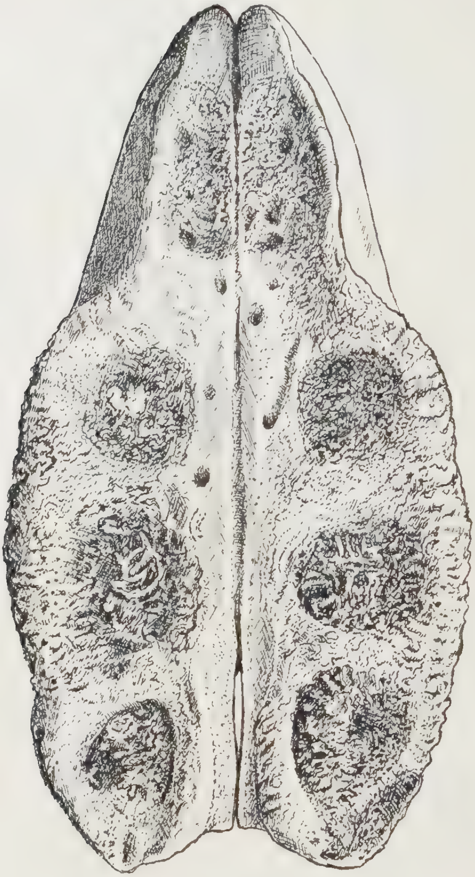

Fig. 138. *Dugong dugong* (Müller). Rostral part of the bent lower jaw seen at right angles on its surface. Nat. size. Zool. Mus. Buitenzorg, no. 56/33. Original drawing by Mrs M. IDENBURG in the collection of dr K. W. DAMMERMAN.

which rests upon it (GREGORY, 1933, p. 401) (see my fig. 67).

Among Selachii the lower jaw of *Scymnorhinus* (*Scymnus*), which is most strongly developed among Selachii, is very high (HOLMGREN & STENSIÖ, 1936, p. 319). We also refer to the following figures in my article: *Squalus* (see my fig. 61), *Chlamydoselachus* (see my fig. 62) and *Isurus* (see my fig. 130 *a*).

For the higher Pisces GREGORY mentions (1933) a number of

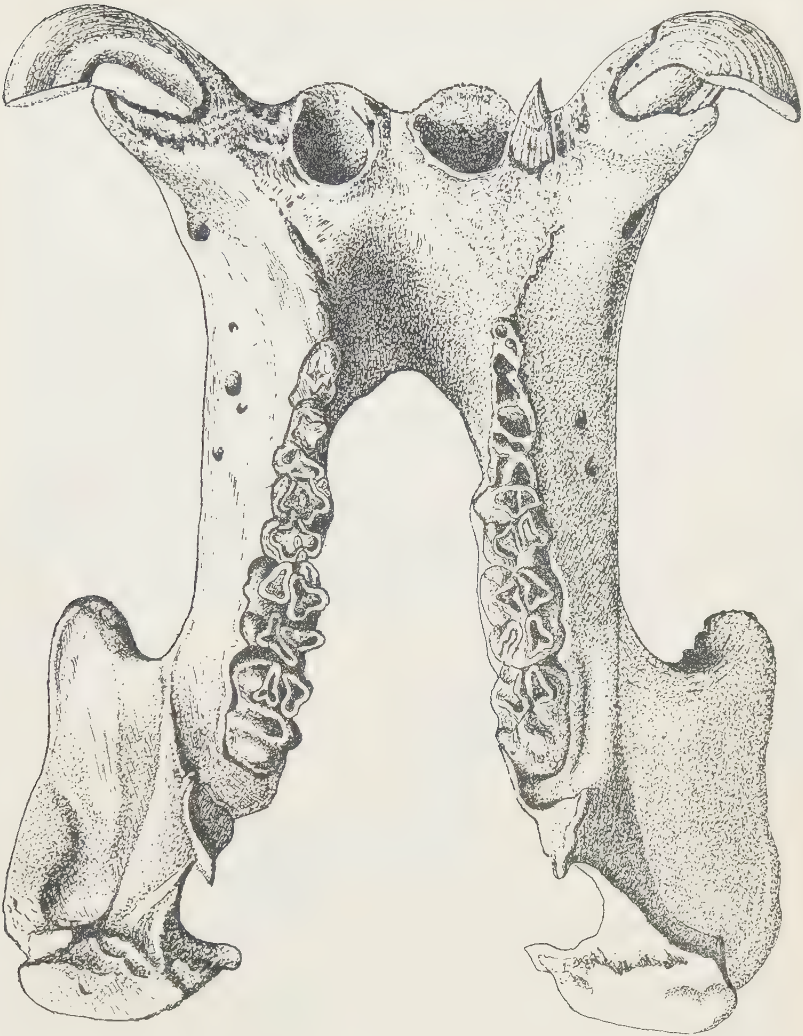

Fig. 139. *Hippopotamus amphibius* L. ♂. 0.22×. Lower jaw seen from above. After DUCROTAY DE BLAINVILLE (1839–1864), Atlas Tome IV, G. *Hippopotamus* Pl. II.

data about the thickness, strength, massiveness *etc.* of the lower jaw, from which conclusions about the height of these lower jaws may be drawn. In *Stylophorus chordatus* Shaw the lower jaw is relatively huge (p. 300, fig. 176), in *Myripristis murdjan* (Forsk.)

it is rather massive (p. 235, fig. 111). In Sparidae with the crushing type of teeth the dentalia are massive; in the pictures referred to, the caudal part of the lower jaw is high, too, *i.e.* in *Archosargus probatocephalus* (Walbaum) and in *Anarhichas* (p. 423, figs 123, 255) (see my fig. 89). In *Gonorhynchus* the lower jaw is relatively stout and shows a relative robusticity (p. 176, fig. 66) (see my fig. 64); in *Chirocentrus* (p. 146, fig. 34) and in *Gymnarchus* the lower jaws are strong (p. 173, fig. 62 B) (see my fig. 82). In *Mormyrops* the dentale is rather thick and, judging from the picture, so is the entire lower jaw (GREGORY, 1933, p. 171, fig. 62 A). In *Lampris* the lower jaw is much thicker than in the primitive *Velifer* (pp. 298/299, figs 173, 174). As an other extreme opposed to these high lower jaws, we mention *Gastrostomus* with its slender rami mandibulares (p. 213, fig. 94) (see my fig. 87) and the Ogcocephalidae where the lower jaw is delicate (p. 401) (see my fig. 67). We also refer to the following figures in this article showing a high lower jaw: *Pseudoscarus* (see my fig. 78); *Tautogolabrus* (see my fig. 81); *Hydrocyon* (see my fig. 86); *Diodon* (see my fig. 121) and *Iniistius* (see my fig. 128). For figures of a low lower jaw we refer to the following figures in this article: *Engraulis* (see my fig. 76); *Tylosurus* (see my fig. 94); † *Cheirolepis* (see my fig. 95); *Osteoglossum* (see my fig. 116); *Lycodontis* (see my fig. 119) and *Chauliodus* (see my fig. 122). Most lower jaws are intermediate (see other figures in this article; see also my fig. 130).

In the higher Vertebrata the height of the lower jaw is strongly dependent on the fact whether the main function of the jaws is seizing, or chopping up of the food. When the chewing-pressure is great, the lower jaw is high, when this chewing-pressure is slight and the main function of the jaws is seizing, the lower jaw is low. We refer for figures of the lower jaw in Amphibia to my figures nrs 31, 96 and 131 and in Reptilia nrs 44, 55, 103, 104, 105 and especially 132.

Among Aves, where the jaws form a pincer-shaped seizing-organ, the lower jaw is low (see my figs 33, 98 and 133). There are, however, a few birds where the lower jaw is high, owing to the fact that the jaws are not only a seizing-organ. In this respect I refer to the following figures in my article: *Ramphastos* (see my fig. 69); *Pelecanus* (see my fig. 106) and *Ara* (see my fig. 133 *i*).

Among Mammalia the differences in height in the lower jaw are very striking, they are most closely connected with the chewing-pressure, and consequently with the development of the teeth and the character of the food (see my figs 47, 58, 60, 70 *a*, 71, 99 *a*, 110 *a*, 111, 112 and especially 134).

Among Mammalia, *Tachyglossus* (*Echidna*) is the genus where the lower jaw is least developed in proportion to the skull and the rest of the skeleton (OWEN, 1866 II, p. 321) (see my fig. 134 *a*). Apart from the Monotremata (see my figs 107 *a*, 134 *a*, *b*) we also notice in other groups where the function of chewing has been eliminated, that the lower jaw is reduced to a narrow rod, as is the case in Cetacea (see my figs 70 *a*, 110 *a*, 134 *v*, *w*, *x*),

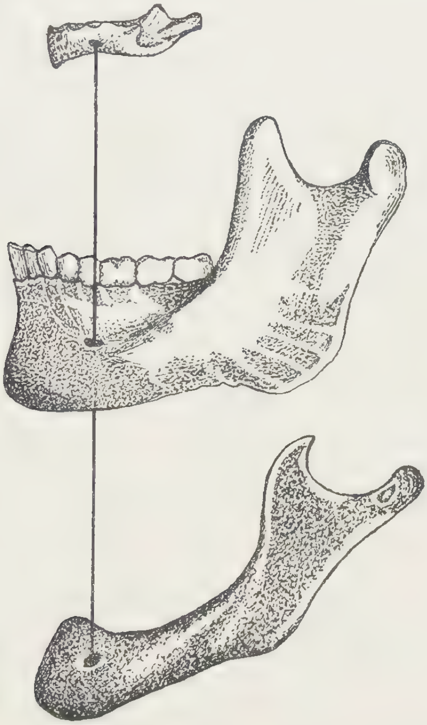

Fig. 140. *Homo sapiens* L. Lower jaws seen from the right side inverted. 0.5×. From above downwards: neonate, adult and senile. After BLUNTSCHLI (1936), fig. 3.

Manis (see my fig. 134 *i*) and Myrmecophagidae (see my fig. 134 *m*) (STADTMÜLLER, 1936, pp. 940, 965, 984).

When the chewing-pressure is very strong, the lower jaw is very high (see especially my fig. 134). In *Homo sapiens* L. the lower jaw is very thick and very high as well, and it is the thickest and strongest component of the facial skull (RAUBER-KOPSCH, 1922, p. 105; 1940, p. 220) (see my fig. 140). This especially holds good for the adult lower jaw, not so much so for the juvenile and senile lower jaw of Man (see my fig. 140; also my figs 113 *a*, 113 *b*).

As we saw, the lower jaw may be locally strongly heightened, such as by the development of a processus coronoideus, by the ramus ascendens of the dentale *etc.*

In Pisces we sometimes find a processus coronoideus and sometimes we don't (see *e.g.* HOLMGREN & STENSIÖ, 1936, p. 415). The processus coronoideus may, in Pisces, be formed by the dentale or by the articulare according to GREGORY (1933, p. 425). According to him, too (1933, p. 425) the processus coronoideus of Pisces with strong-biting or pincers-like jaws is usually large or massive in proportion to the length of the lower jaws. He refers to pictures of *Distichodus langi* Nichols & Griscom, which show a high, ascending bar of the articulare (p. 185, fig. 71), of *Spheroides stictonotus* (Temm. & Schl.) where the processus is evidently situated on the articulare (fig. 167), of *Hoplegnathus* where it is evident that the same occurs (p. 250, fig. 124) and of *Pseudoscarus guacamaia* (Cuv.), which shows an ascending processus of the dentale (p. 258, fig. 133) (see my fig. 78). An ascending processus or ramus of the dentale occurs in very many Pisces, at least if we regard the caudally ascending upper edge of the dentale as such (GREGORY, 1933, pp. 176, 187, 190/191, 193, 257/258). I refer also to my figs 27, 29, 80 and 81, showing a processus coronoideus and, as regards a caudally ascending upper edge of the dentale, to my figs 19, 77, 79, 82 and 128. Often the upper edge of the caudal part of the lower jaw is heightened too. For Xenopterygii GREGORY (1933, p. 371) mentions especially that here the vertical and very stout ascending processus of the articulare indicates powerful adductor muscles. In *Opsanus tau* (L.) the thick processus surangularis of the articulare together with the stout, ossified MECKELian region of the articulare afford insertion for the adductor muscles (GREGORY, 1933, p. 383). In *Astroscopus* *y-graecum* (C. V.) the dermarticulare is suddenly expanded downward, below the quadratum-articulare joint; it probably afforded insertion just in front of this expansion to the transverse muscles of the lower jaws (Gregory, 1933, p. 370, fig. 247) (see my fig. 42).

Also in Reptilia (see my fig. 132) the processus coronoideus is not everywhere formed by the same osseous element, generally it is formed by the coronoid. In † Cynodontia the processus coronoideus is situated on the dentale; this displacement of the insertion of the chewing-muscles to the dentale is combined with a modification of the structure of the entire lower jaw and is connected with a change of the other places of origin of the musculus temporalis and with the altered situation of the jaw joint; in their turn all these alterations are connected with the enlargement of the cerebral capsule in the † Cynodontia (Versluys, 1936, pp. 752/753). The height and the general development of the processus coronoideus in Reptilia depends on the development of the musculus temporalis (Versluys, 1936, p. 749).

Also in the Mammalia (see my fig. 134) the size of the processus coronoideus is connected with the development of the musculus temporalis and, consequently, with the function of the lower jaw (Stadtmüller, 1936, pp. 976, 982). Connected with the latter function is also the size of the processus articularis *s.* condyloideus in Mammalia. As Schimkewitsch (1921, quoted after Stadtmüller, 1936, p. 940) said, the facts whether the processus ascendens of the lower jaw makes a clear angulus mandibulae with the lower jaw or no, and whether, consequently the joint is situated higher than the chewing-plane or no, and whether the chewing-pressure is equally distributed or no, all depend on herbivory, respectively carnivory (Stadtmüller, 1936, pp. 971, 972, 974, 989). Concerning *Equus caballus* L. Marinelli (1933, p. 217) (see my fig. 134 *kk*) mentions that the occurrence of the angulus mandibulae increases the surface for the insertion of the chewing-muscles.

In a small number of cases there is also a local heightening of the lower jaw caused by the development of a process-like structure on the ventral edge of the lower jaw. Sometimes it is found in the caudal part of the lower jaw (see my figs 111, 134 *n*, *q* and *dd*). In another case in the rostral part of the lower jaw (see my fig. 134 *y*).

c. The position of the lower jaw

The position of the lower jaw is not always identical in one and the same animal, because the lower jaw can be moved with regard to the upper jaw. In some species of animals a second cause is added to this, *viz.* the ability to move the two halves of the lower jaw with regard to each other in the symphysis mandibulae, by which the position is altered.

The position of the lower jaw is especially of importance with regard to the upper jaw. When the mouth is closed the position of the lower jaw adapts itself to that of the upper jaw. In a number of cases, however, the ventral edge of the upper and the dorsal edge of the lower jaw do not run parallel, neither in the longitudinal nor in the transverse direction. As examples we mention a number of fishes (see my figs 78, 91, 117, 121) and the *Mystacoceti.* When discussing the length, we already pointed out in the above that the lower jaw reaches farther backward than the upper one, that, as a rule, the lower jaw reaches as far forward as the upper jaw, but we also got to know some exceptions where the lower jaw reaches farther forward or not so far forward. The position of the lower jaw also adapts itself to that of the upper one as regards the transverse direction. This is connected with the fact that the teeth or the teeth and back-teeth

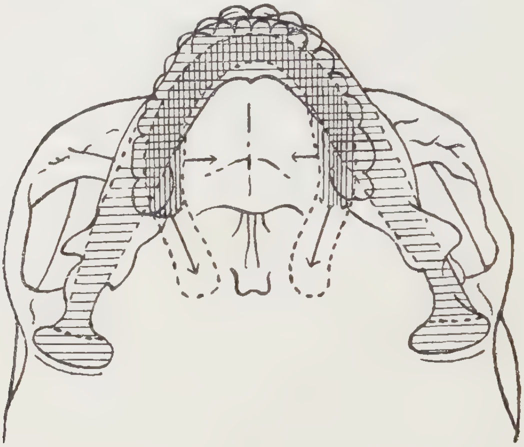

Fig. 141. *Homo sapiens* L. Rostral part of the skull in ventral view showing the lower jaw and new upper jaw in their relative position. After Bluntschli (1936), fig. 7.

of the upper jaw fit upon those of the lower jaw. This does not imply that the teeth are placed straight opposite to one another; they can also fit upon each other somewhat obliquely in a lateral direction (see my fig. 141).

It must also be noted that the position of the lower jaw with regard to the primary rostrum is as little defined as was the case with the upper jaw. We can only say that the primary rostrum reaches farther rostralward (see my figs 61, 74). As regards the position of the lower jaw with regard to the secondary rostrum, the rostral tip of the lower jaw will, by virtue of the definition of a secondary rostrum, remain caudal of it, at least when the lower jaw reaches as far rostralward as the upper jaw.

Seeing that special stress is laid on this, we also want to point out that, in *Stylophorus chordatus* Shaw, according to GREGORY (1933, p. 299, fig. 176) the very long lower jaw projects backward behind the gill region in a sharp elbow.

The indication of the slope of the lower jaw may also serve as an important datum on the position of the lower jaw. When the mouth is closed, however, the slope of the lower jaw will adapt itself to that of the upper one. Therefore we may refer to the exhaustive discussion of this and shall limit ourselves here to the few cases where GREGORY (1933) emphatically points out the slope of the lower jaw. GREGORY mentions a sloping lower jaw matching an upper jaw with an identical slope for *Chirocentrus* with its upturned lower jaw (1933, p. 146, fig. 34), *Zeus* with its marked upturning of the lower jaw (pp. 271/272, fig. 148), the Gobioidei, where the lower border of the lower jaw is directed only moderately upward (p. 346, fig. 226) and *Astroscopus* where the lower jaw is inclined sharply upward (p. 369, fig. 247) (see my fig. 42). In other cases, however, the general slope of the lower jaw does not agree with the slope of the lower edge of the new upper jaw. Such is the case in *Dorosoma* (*Chatoëssus*) where the lower jaw is directed sharply upward, but the lower edge of the short new upper jaw runs practically horizontal (p. 147, fig. 39) (see my fig. 29) and in *Angelichthys* and *Pomacanthus* with an upward inclination of the lower jaw, which lies nearly in a direct line with the axis of the new upper jaw, which is connected with the great development of the teeth in both jaws (p. 278, figs 153, 154). To this we may add the information that the lower jaw does not always form a straight line. Thus *Capros aper* (L.) shows a sharp downward turn of the dentale on the articulare (GREGORY, 1933, p. 273, fig. 149).

A curious feature occurs in *Halicore* (see my fig. 142), where the ventral edge of the upper jaw runs parallel to the dorsal edge of the lower jaw, when the mouth is closed, but the lines of the edges in both jaws show a bent.

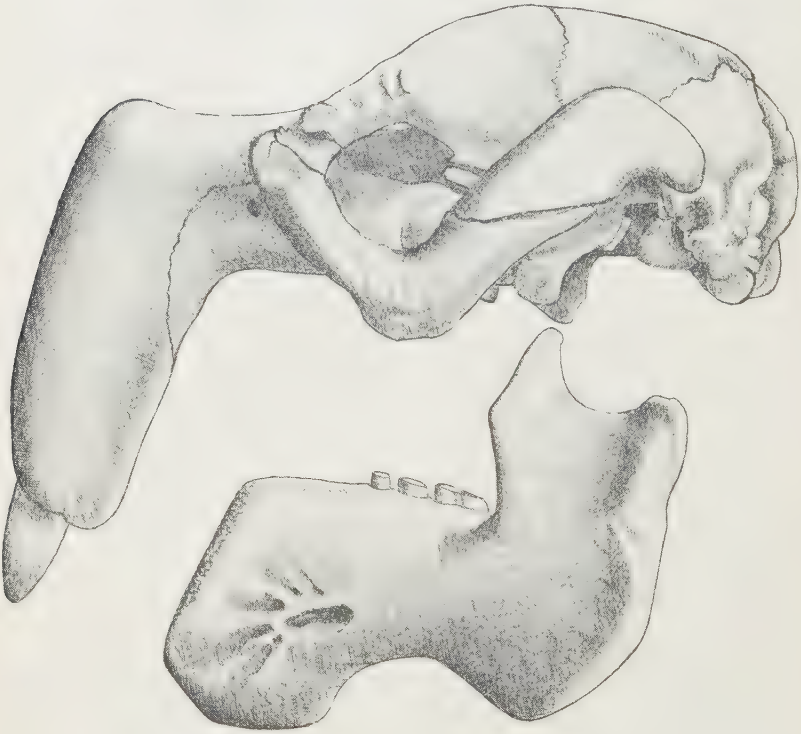

Fig. 142. *Dugong dugong* (Müller) ♂. Skull with lower jaw seen from the right side inverted. 0.3×. Zool. Mus. Buitenzorg, no. 56/33. Original drawing by Mrs M. IDENBURG in the collection of dr K. W. DAMMERMAN.

d. Homology and non-homology

In judging the size, and especially also the position of the lower jaw, we must bear in mind that, within the Vertebrata, lower jaws are three different morphological formations.

In Elasmobranchii the lower jaw is the cartilaginous mandibula, in the higher Non-Mammalia the lower jaw may be derived from this but shows a number of covering bones together with ossifications of cartilage, whereas in Mammalia the lower jaw is something different still. This is so according to the theory of REICHERT according to which the lower jaw of the Mammalia is said to consist only of the dentale of the Non-Mammalia. According to the idea, first mentioned by VAN KAMPEN (1904, p. 364 footnote) the dentale reached as far as the quadratum-articulare joint during the transition from Non-Mammalia to Mammalia.

In the above we already pointed out that the processus coronoideus is not everywhere homologous either.

7. JAW JOINT

a. Introduction

Owing to its slight absolute and relative size the jaw joint hardly plays a part with regard to space in the architecture of the skull, but its situation makes the part it plays extremely important.

b. The size of the jaw joint

The literature consulted gave no or hardly any exact data about the size of the jaw joint.

The absolute size of the jaw joint

In general we may conclude that the size of the jaw joint runs parallel with that of the lower jaw. A lower jaw which is large in absolute measurements will be hung up on a large joint (see f.i. my figs 58, 69, 106 *a*, 113 *b* and 142). With a very thin, rod-shaped lower jaw the joint will be small too (see f.i. my figs 33, 107 *a*).

The shape of the jaw joint, or at any rate that of the condylus will influence the absolute size of the jaw joint. When the cubic content is the same, the surface of a ball-and-socket joint will be smaller than that of the cylindrical condylus of a hinge joint (see f.i. my figs 136, 139). These things are connected with the way in which the lower jaw is moved with regard to the upper jaw (BÖKER, 1937, pp. 158, 160).

The relative size of the jaw joint

The factors bearing upon the absolute size of the jaw joint, mentioned above, also influence the relative size (see my fig.

140). On this subject too, direct data are absent from the literature consulted.

c. The position of the jaw joint

In the discussion of the position of the jaw joint we shall successively treat the situation in a rostrocaudal direction, then that in a dorsoventral direction, and finally that in a mediolateral direction. We shall conclude with some data on the position of the axis of the jaw joint.

In a rostrocaudal direction, the position is indicated with regard to the rostrocaudal measurement of the entire skull, moreover it is more accurately indicated with regard to the orbita.

With regard to the rostrocaudal measurement of the entire skull the position of the jaw joint in Pisces is rather varying. As GREGORY discusses the situation of the jaw joint with regard to the orbita, in Pisces, very exhaustively (1933), we shall here limit ourselves to a single observation, derived from HOLMGREN & STENSIÖ (1936, pp. 398/399, 415, 420, 426), who point out that in † Palaeoniscidae and † Belonorhynchidae († Saurichthyidae) the hyomandibulare and the praeoperculum show a very pronounced slope from upper front to lower back, so that the jaw joint has a very far caudal position, that this is less markedly the case with Perleididae, and even less so in Ospiidae. Later on we shall discuss this slope of the hyomandibulare and the praeoperculum and its connection with the position of the jaw joint, more fully.

Among Amphibia and Reptilia the position of the jaw joint is sometimes very far backward, sometimes it is situated in the extreme ventrocaudal corner of the skull, as is *e.g.* the case in *Rana*, *Crocodylus* and *Python* (see my figs 20, 101 *a*; see also my figs 31, 96 *b*, 102 *a*, 104, 105).

This far caudal position of the jaw joint in Anura develops during metamorphosis from a more rostral position in larvae (LUBOSCH, 1938, p. 1033).

Even if the jaw joint does not occupy such an extremely backward position (see my figs 44, 45), it is all the same lateral of the hyoid arch and the auditory ossicles although, morphologically, the mandibular arch lies rostral of the hyoid arch and the auditory ossicles.

In † Cynodontia and in Aves (see my figs 13, 34, 56, 69, 98) the jaw joint does not lie so far backwards, which must be attributed to the great development of the brains, by which the cerebral capsule extends in a caudal direction (VERSLUYS, 1936, pp. 752/753; MARINELLI, 1936, p. 810). An exception, however, is a.o. *Caprimulgus* (see my fig. 33) and *Pelecanus* (see my fig. 106 *a*).

In Mammalia the jaw joint does not lie far caudal in the skull either (see my figs 58, 60, 71, 99 *a*, 112, 113 *a*, *b*). Here, too, this relatively rostral position is probably due to the powerful development of the brain, by which the cerebral capsule extends in a caudal direction. The explanation might also partly be sought in the fact that, according to the followers of the theory of REICHERT, the jaw joint lies, in Mammalia, rostral of the old jaw joint of Non-Mammalia, even though, according to later followers of REICHERT's theory, the jaw joint of Mammalia originated in the place of the old jaw joint and with its cooperation.

Also within Mammalia, even within a comparatively small systematic group, not inconsiderable differences are found in the position of the jaw joint, which lies more or less far rostral. Thus, in the phylogeny of Equidae the region of the jaw joint is displaced forward with regard to the back of the head, together with the back edge of the lower jaw, this might be connected with a difference in the carriage of the head (MARINELLI, 1933, pp. 217/218).

Much more detailed are the data on the position of the jaw joint in Pisces in a rostrocaudal direction with regard to the orbita. The material point is then the antero-posterior placement of the quadratum-articulare centre, which GREGORY (1933, p. 420) defines as its distance in front or behind the projection of the mid point of the hyomandibulare socket upon the horizontal (see my fig. 143). In this definition the "horizontal" is the line joining the prosthion (*i.e.* the most anterior point of the snout) and the pygidion (*i.e.* the mid point of the narrowest part of the caudal peduncle). Now this point is situated immediately behind the back edge of the orbita, so that, in practice, the position with regard to the orbita is a point more easily to be handled.

With regard to the position of the quadratum-articulare joint with regard to the orbita, we can distinguish three groups of conditions, *viz.* the quadratum-articulare joint is situated behind the vertical through the back edge of the orbita (see my fig. 143 *a*, *b*),

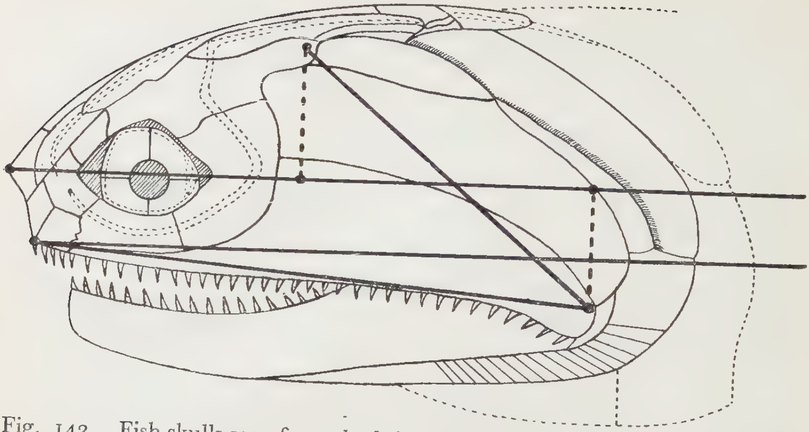

Fig. 143. Fish skulls seen from the left side in which are drawn the horizontal through the prosthion, the line connecting the mid point of the hyomandibulare socket with the mid point of the quadratum articulare joint, the line connecting the latter point with the foremost point of the new upper jaw, the projection of the mid point of the hyomandibulare socket, of the mid point of the quadratum articulare joint and of the foremost point of the orbita on the horizontal. Fig. 143 *a* shows two horizontal lines, one through the prosthion, the other through the foremost point of the new upper jaw. All skulls are drawn to about the same length.

a. Cheirolepis traill Agassiz. After GREGORY (1933), figs 12 A, 286 A.

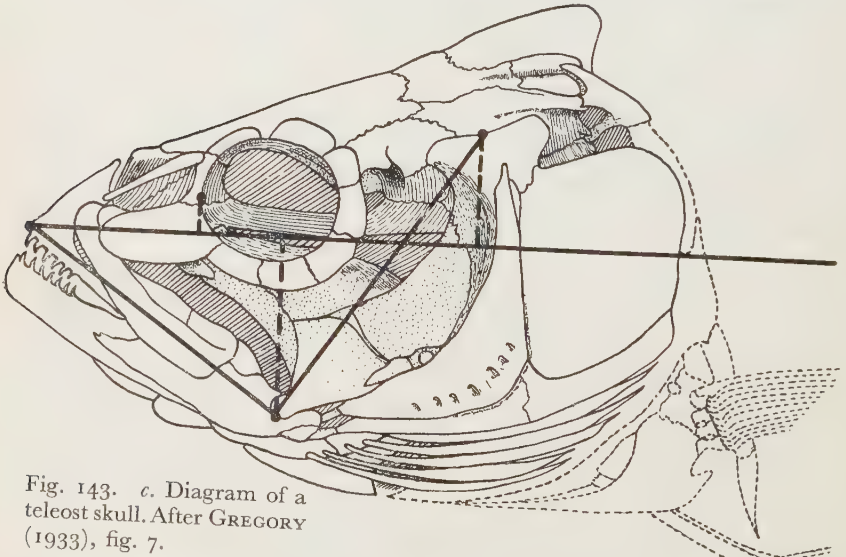

Fig. 143. *c.* Diagram of a teleost skull. After GREGORY (1933), fig. 7.

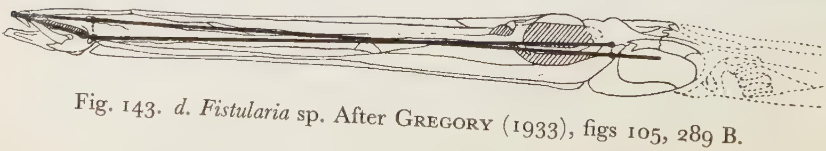

Fig. 143. *d. Fistularia* sp. After GREGORY (1933), figs 105, 289 B.

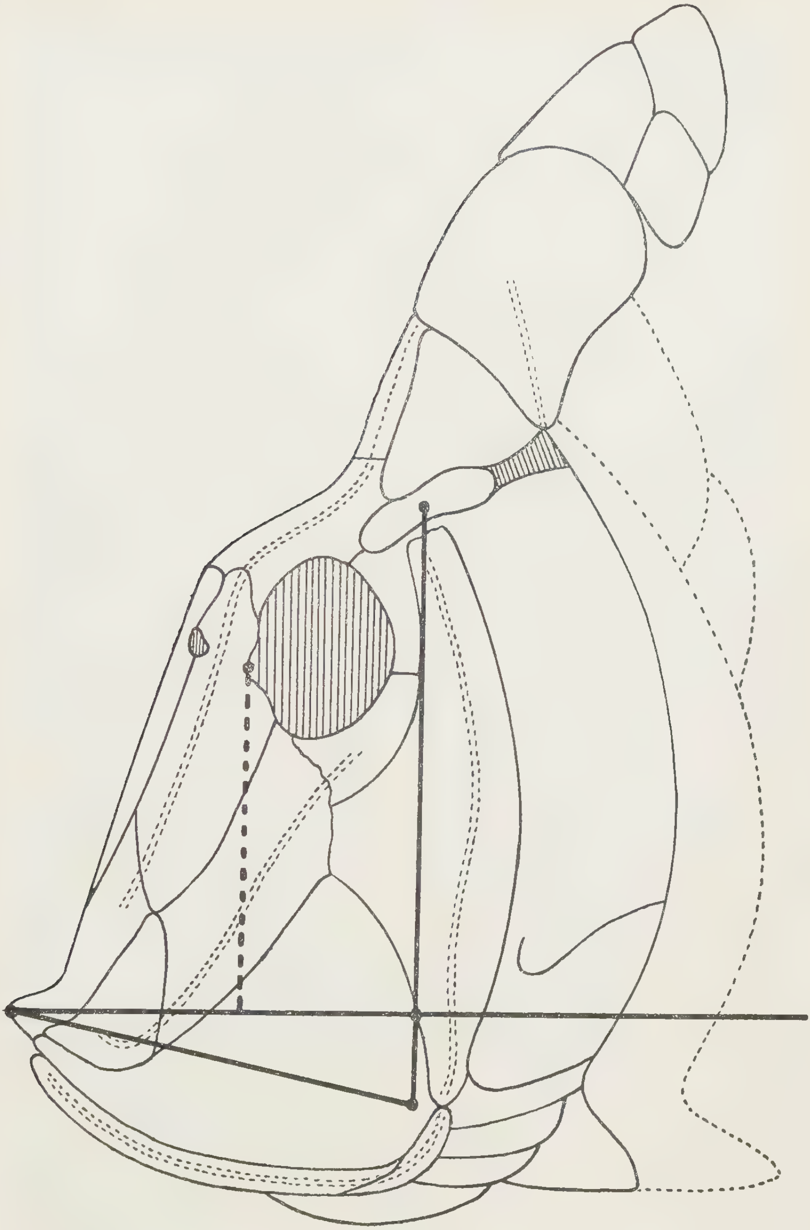

Fig. 143. *b. Platysomus parvulus* Williamson. After GREGORY (1933), figs 15, 286 D.

it is situated ventral of the orbita (see my fig. 143 *c*) or it is situated rostral of the vertical through the front edge of the orbita (see my fig. 143 *d*).

The position of the quadratum-articulare joint caudal of the vertical through the back edge of the orbita, so a backward position of the quadratum-articulare joint, is found among Pisces with a primitive condition of the skull, such as † *Cheirolepis* (p. 421, fig. 286 A, see also figs 12 A, 283 A) (see my figs 95, 143 *a*), as may also be derived from the data on the slope of the suspensorium. We also find this condition in the allied † *Coccocephalus* (fig. 286 B, see also figs 12 C, 283 B), † *Palaeoniscus* (fig. 12 B) and in † *Perleidus* (fig. 286 C). In † *Platysomus* the quadratum-articulare joint is situated very little behind the back edge of the orbita (fig. 286 D, see also fig. 15 B) (see my figs 90, 143 *b*). Among Teleostei such a more caudal position of the quadratum-articulare joint is an exception according to GREGORY (1933, p. 422). Such an exceptional backward displacement of the quadratum-articulare joint is especially mentioned by GREGORY (1933, p. 422, see also p. 418) for *Engraulis encrasicholus* (L.), where the quadratum-articulare joint lies well behind the orbita (p. 147, fig. 40) (see my fig. 76), *Lycodontis funebris* (Ranzani) (fig. 82 B) (see my fig. 119), *Gonostoma elongatum* Gthr (fig. 53), *Stomias boa* (Risso) (fig. 56), their allies and some others, among which *Gastrostomus* (fig. 94) (see my fig. 87) is especially mentioned. But GREGORY (1933) also mentions it for *Polynemus*, which shows a backward displacement of the quadratum-articulare joint to a point almost directly beneath the mid point of the hyomandibulare, *i.e.* caudal of the back edge of the orbita (p. 268), and for *Ophicephalus*, where the quadratum-articulare joint lies far behind the eye (pp. 269/270, fig. 145 A). So much may be derived from direct data in GREGORY's text. The number of cases where the quadratum-articulare joint lies caudal of the vertical through the back edge of the orbita, is, of course, even greater. We might derive even more examples from the data on the direction of the suspensorium in the text, and especially from the pictures in GREGORY. But we shall not do so, and conclude with pointing out that the third main type, discussed before, of the proportion of the length of the snout to the length of the upper jaw, furnishes many examples. In this third main type the snout is short, whereas the upper jaw is long. Some cases from this third main type, however, do not show this extreme caudal position of the quadratum-articulare joint, *viz.* where the direction of the upper jaw is extremely steep, so that the quadratum-articulare joint lies ventral of the orbita, as is perhaps the case in † *Pholidophorus macrocephalus* Agassiz with its far ventrally situated orbita (p. 136, fig. 29). To mention a single example from this third main type, where the quadratum-articulare joint lies far caudal of the orbita, we point to *Osteoglossum* (fig. 57) (see my fig. 116), *Synodus foetens* (L.) (fig. 86), *Saurus myops* (Bl. Schn.) (fig. 87 A) and *Symbranchus marmoratus* Bl. (fig. 231) (see my fig. 123).

In other cases the quadratum-articulare joint lies below the orbita (see my fig. 143 *c*). According to Gregory (1933, p. 421) the Teleostei appear to have been derived from groups wherein the quadratum-articulare joint has a more rostral position as follows from the data on the direction and course of the suspensorium. Gregory refers to his picture of † *Acentrophorus* where the quadratum-articulare joint is situated under the back edge of the orbita (fig. 287 A, also fig. 21 B). This more rostral position of the quadratum-articulare joint remains in later Teleostei, even when the jaws show such a great secondary elongation as is the case in *Tylosurus*, where the quadratum-articulare joint lies under the back edge of the orbita (pp. 421/422, also p. 418, fig. 289 A) (see my fig. 94). In the Carangidae it is highly probable that in the primitive Carangid the quadratum-articulare joint was moderately far forward, perhaps beneath the middle of the orbita, and that, with more predaceous habits one of the possibilities for enlargement of the mouth lay in a moderate backward shifting of the quadratum-articulare joint as in *Coryphaena*; but in this *Coryphaena* the position of the quadratum-articulare joint is still under the back edge of the orbita (p. 302, fig. 183). From the pictures indicating more especially the position of the vertical through the quadratum-articulare joint with regard to the orbita (figs 287, 288), and from Gregory's information in the text (1933) we may, in addition derive the following. Under the back edge or under the back half of the orbita lies the quadratum-articulare joint in † *Portheus* with its anteriorly placed quadratum-articulare joint (p. 144, fig. 288 B, see also fig. 36), further in *Chirocentrus* (fig. 288 C); in † *Hoplopteryx lewesiensis* (Mantell) the quadratum-articulare joint lies almost directly beneath the posterior border of the orbita (p. 233, fig. 110) while in *Tarpon atlanticus* (C. & V.) with its forward position of the quadratum-articulare joint it lies under the back edge of the orbita (p. 138, fig. 31) (see my fig. 85). In † *Leptolepis* (fig. 288 A) and in † *Semionotus* (fig. 287 B) the quadratum-articulare joint lies about beneath the centre of the orbita. † *Semionotus* is mentioned with † *Dapedius*, † *Lepidotus c.s.* among the Triassic and later genera of the Semionotidae, showing a forward migration of the quadratum-articulare joint (pp. 125/127, fig. 22 A). In † *Antennarius* which, like allied Pediculati shows a marked forward displacement of the quadratum-articulare joint, it lies beneath the front edge of the orbita (p. 393, fig. 288 D, see also figs 265, 266). In *Priacanthus* the quadratum-articulare joint is brought forward to near the anterior border of the eye and according to the picture it may perhaps reach slightly rostral of the front edge of the orbita (p. 247, fig. 120). In *Hoplegnathus* the quadratum-articulare facet is located far forward, beneath the anterior border of the orbita (p. 250, fig. 124). In *Dorosoma* (*Chatoëssus*) the lower end of the suspensorium lies in front of the lower border of the orbita, but, according to the picture, still under the front edge of the orbita (p. 147, fig. 39) (see my fig. 29). Also in *Albula* the lower end of the suspensorium is dragged forward, and, according to the picture, the quadratum-articulare joint lies ventral of the front edge of the orbita (p. 144, fig. 37) (see my fig. 125).

Rostral of the vertical through the front edge of the orbita lies the quadratum-articulare joint in a number of other Pisces (see my fig. 143 *d*). In the above we saw that the more rostral position of the quadratum-articulare joint persists in later Teleostei. Sometimes the quadratum-articulare joint in these cases is situated rostral of the front edge of the orbita. This is even the case in genera where the jaws show a secondary elongation, such as *Lepisosteus* (Gregory, 1933, p. 421, fig. 287 D, see also fig. 24 A; Holmgren & Stensiö, 1936, fig. 363) (see my fig. 65). In *Sternoptix* the quadratum-articulare joint lies below and in front of the orbita, according to the picture rostral of the front edge of the orbita (p. 158, fig. 52). In *Gymnarchus* the eye lies above and slightly behind the quadratum-articulare joint, and according to the picture the quadratum-articulare joint lies immediately before the front edge of the orbita (p. 173, fig. 62)(see my fig. 82). *Zeus* shows a forward growth of the quadratum-articulare pivot which, according to the picture lies before the vertical through the front edge of the orbita (p. 272, fig. 148). In

Periophthalmus the quadratum-articulare joint has moved forward in front of the anterior orbital rim (p. 347, see however fig. 228) (see my fig. 41). In *Microspathodon* the quadratum-articulare joint lies remarkably far forward in front of the anterior border of the orbita (p. 255, fig. 128). This collection of examples from GREGORY might be enlarged, if we should also take into account the data on the course and direction of the suspensorium, and especially the pictures. We shall, however, limit ourselves to direct information given by GREGORY. The same is the case with examples of the first main type of the proportion of the length of the snout to the length of the upper jaw, in which main type the snout is long and the upper jaw is short. All these cases are examples of an exceptional far forward position of the quadratum-articulare joint. We shall here, too, limit ourselves to direct information given by GREGORY (1933). In "Balistoidae" (p. 422, fig. 290) and in *Fistularia* (p. 418, fig. 289 B) (see my figs 93, 143 *d*) the quadratum-articulare joint shows an exceptional far forward position. In the process of the shifting of the mouth farther forward, from Chaetodontoidae up to "Teuthidoidea", Zanclidae and Balistidae, the quadratum-articulare joint is finally produced to a point far in front of the eye (p. 282, figs 158–162). In *Gasterosteus trachurus* C. & V. the quadratum-articulare joint lies well in front of the preorbital border (p. 224).

In a dorsoventral direction the position of the jaw joint is indicated with regard to the height of the entire skull, with respect to the jaws and to the orbita.

Regarding the dorsoventral position of the jaw joint with respect to the entire skull, we want to point out that GREGORY (1933, p. 420) defines the level of the quadratum-articulare centre as its distance below the horizontal; the horizontal being the line joining the prosthion (*i.e.* the most anterior point of the snout) and the pygidion (*i.e.* the mid point of the narrowest part of the caudal peduncle) (see my fig. 143). In the text GREGORY (1933) gives some information about this position of the quadratum-articulare joint in Pisces. *Tarpon atlanticus* (C. & V.) shows a depth of this joint (p. 138, fig. 31) (see my fig. 85). † *Portheus* shows a depressed quadratum-articulare joint (p. 144, fig. 36). In *Osteoglossum* the quadratum-articulare joint grew downward (p. 164, fig. 57) (see my fig. 116), in *Polynemus* it shows a downward displacement (p. 268), and *Zeus* shows a downward growth of the quadratum-articulare pivot (p. 272, fig. 148). In † *Hoplopteryx lewesiensis* (Mantell) and in *Lachnolaimus* the quadratum-articulare joint lies at a low level (pp. 233, 257, figs 110, 130) (see my fig. 129). In *Capros aper* (L.) the quadratum-articulare joint is depressed far below the usual level (p. 273, fig. 149 A). *Antennarius* and allied Pediculati show a marked and excessive downward depression of the quadratum-articulare joint (pp. 391, 392, 393, figs 265, 266).

In the best known Amphibia (see my figs 20, 31, 96 *b*), Reptilia (see my figs 44, 45, 55, 103, 104, 105) and Aves (see my figs 13, 33, 34, 56, 69, 98, 106 *a*) the jaw joint lies far ventral in the skull.

In Mammalia the height of the processus ascendens must influence the position of the jaw joint in a dorsoventral direction (see my figs 113 *a*, *b*, moreover 60, 71, 99 *a*, 107 *a*, 112, 142).

The position of the jaw joint with respect to the jaws, is generally such, that the jaw joint lies caudal of the jaws because the jaws run horizontal or have only a very slight upward or downward slope.

In a number of Pisces, however, the jaws show such a marked slope that the jaw joint lies almost ventral of the jaws. Gregory (1933, p. 369, fig. 247) (see my fig. 42) mentions that in *Astroscopus y-graecum* (C. V.) the quadratum-articulare joint is drawn forward so as to be only a little way behind the strongly upturned mouth, and of *Chaetodon* he mentions (p. 279, fig. 155) that the quadratum-articulare fulcrum is brought far below the mouth. A similar condition occurs in very many other Pisces, and many more examples might be derived from the pictures given by Gregory (see f.i. my fig. 29).

The situation of the jaw joint with respect to the orbita is not specially discussed by Gregory (1933). If, however, a connection is laid between the slope of the upper jaw and the level of the quadratum-articulare joint with regard to the horizontal (combined with the length of the snout) the level with regard to the orbita is, in my opinion, more important than that with regard to the horizontal. I shall here limit myself to pointing out that, in the above (pp. 256—258, 264) we used already this level with regard to the orbita in classifying the conditions occurring in the main class C mentioned before, as well with regard to the caudal extension of the back edge of the new upper jaw, as especially with regard to the slope of the new upper jaw in connection with the position of the orbita. For examples of an advanced dorsal or ventral position of the quadratum-articulare joint with regard to the orbita in a dorsoventral direction, we may refer to the examples given there.

For the position of the jaw joint in a mediolateral direction, we may in the first place refer to the data on the breadth of the jaws as far as this could be derived from the data on the distance between the right and the left jaw joint. Apart from the direct data concerning this distance collected in the discussion of the upper jaw, we also gave a number of data on the breadth of the mouth cavity and the slit of the mouth, from which the distance between the two jaw joints may be derived as well. So we shall here limit ourselves to data that were not included there.

Among Mammalia the jaw joint of *Giraffa camelopardalis* (L.) is said to be situated far medially (MARINELLI, 1933, pp. 210, 211). In Pecora in general the jaw joint lies far medially (MARINELLI, 1933, p. 205). This would be contrary to what we find in recent Equidae where the fossa glenoidea lies much more laterally, as is *e.g.* the case in *Equus caballus* L.; this lateral position developed in fossil Equidae from a more medial position, in the course of dhylogeny (MARINELLI, 1933, p. 218).

In the adult *Loxia curvirostra* L. the jaw joints have an asymmetrical position (BÖKER, 1937, p. 27).

As regards the position of the axis of the jaw joint, as it may be called when we have to deal with an elongated form of this joint, we find several conditions. Sometimes the axis is transverse (Rodentia), sometimes oblique (Rodentia, *Homo*, see my fig. 141), sometimes longitudinal. The direction of this axis has great influence on the possibility of movement of the lower jaw (BÖKER, 1937, pp. 158, 160).

d. Homology and non-homology

In judging the size, but more especially the position of the jaw joint we must bear in mind that this joint is not, or not completely homologous in Mammalia and Non-Mammalia (quadratum-articulare joint opposite squamosum-dentale joint).

8. SUSPENSORIAL MECHANISM OF THE UPPER JAW

a. Introduction

In order to suspend the upper jaw to the cerebral skull, and nothing more, some tendons and ligaments would be sufficient, because their construction makes them resistant to pull and torsion, just like bone and cartilage. But bone, and cartilage more or less, are constructed to withstand pressure as well. As MARINELLI (1929, p. 129) expresses it: bone has been given to the animal's body to withstand pressure ("Knochen ist im Tierkörper dazu da, einen Druck auszuhalten"). And as the demands made on the suspensorial mechanism of the upper jaw to the cerebral skull are not only those of withstanding pull and torsion, but also pressure (in biting and chewing) a skeletal suspension of the upper jaw to the cerebral skull is seen to appear.

The suspensorial mechanism of the upper jaw in Elasmobranchii must be different from the other Vertebrata, because the upper jaw is different; in Elasmobranchii the palatoquadratum functions as upper jaw, in the higher Vertebrata the new upper jaw appears consisting of praemaxillare and maxillare.

According to MARINELLI (1936, pp. 230/231) there is, however, another reason why the suspensorial mechanism is so different in the two cases. According to him a pressure in biting and chewing – and, as a matter of fact a regular movement of the jaws – only occurs when the upper jaw (whether in its entirety or on some points of especial importance in biting and chewing) is solidly supported by a pillar or piers with regard to the origin of the chewing-muscles (the same holds good for the jaw joint). Now, in Elasmobranchii these three points (dental plate, jaw joint and place of insertion of the chewing-muscles) all lie on one and the same piece of the skeleton, *viz.* the palatoquadratum and so the influence of the suspensorial mechanism of the upper jaw to the cerebral skull on the structure of this cerebral skull is slight. In higher Vertebrata, however, these three points lie on different skeletal elements, and other parts of the skull lie between the place of origin of the chewing-muscles and the dental plate (the elements of the new upper jaw bearing the teeth); the same holds good for the jaw joint. For this reason certain lines of construction occur in the skull, dependent on the size of the skull and the intensity of the power used in biting and chewing. These lines finally influence the entire structure of the skull (MARINELLI, 1936, pp. 230/231; see the picture in Böker, 1937, fig. 199 of *Homo*) (see my fig. 144).

Consequently this influence of the suspension of the jaws on the structure of the skull may be regarded as extremely far-reaching. We can, as Marinelli observes (1929, p. 128), regard the skull as a whole, as a mechanical construction complete in itself, the main function of which is the seizing and chopping up of food or prey. Marinelli (1929, pp. 130, 131, 132) expresses it thus, that the new upper jaw is mainly suspended to the stout roof of the skull by means of the side-parts of the facial skull, and via this roof to the occipital region of the skull. To this we can add an observation of Gregory's (1933, p. 286) in connection with the conditions found in *Balistes*, that the figure of this highly specialized fish particularly well illustrates something that is true of all Vertebrata namely, that the back part of the skull serves as the anchor or pivot for two sets of stresses, one coming from the locomotor apparatus behind (in connection with the attachment of muscles of this locomotor apparatus) and another from the jaws and branchial apparatus, in front and below the occiput (see my fig. 43). In the Sparidae, where teeth and jaws are very powerful, we find an equally great massiveness and strength of the ethmo-vomer block, the interorbital bridge, the cranial vault and the parasphenoid (Gregory, 1933, p. 438) (see my fig. 89). Of other large-mouthed, predaceous Pisces, Gregory (1933, p. 438) says that the stiffening of the ethmo-vomerine block and of the interorbital bridge is connected with the powerful development of the teeth on the vomer. Even when we consider only a part of the new upper jaw we come to far-reaching conclusions as regards the structure of the skull. Let us, *e.g.* regard the preorbital part of the new upper jaw. The pressure exercised on this part of the new upper jaw will be transmitted to the places of attachment of the chewing-muscles. So we see that the pressure lines found in front of the orbita, run to the lateral sides of the teeth and continue across the bridge of the nose into the roof of the forehead and even farther backward into the region of the places of origin of the chewing-muscles, sometimes even strengthened by a well developed crista sagittalis (Marinelli, 1929, p. 136; 1933, p. 212). If, to mention a second example, we regard the region of the most backward teeth, we see, that generally the skull is firmly constructed in the region over this row of teeth (Marinelli, 1929, p. 133).

In this discussion, however, we will neither limit ourselves to vague generalities, nor discuss all the consequences of the suspension of the upper jaw for the entire skull. We shall especially pay attention to the formations of the upper jaw, with which it is suspended to the cerebral skull, and to the parts of the cerebral skull which are in direct contact with the upper jaw. In doing so we shall, as Marinelli indicates (1933, pp. 203, 204, 210, 211, 221; see also 1929, p. 129), consider the different parts and elements of the suspensorial mechanism of the upper jaw, which have each a task of their own and form a construction element with an individual shape of its own.

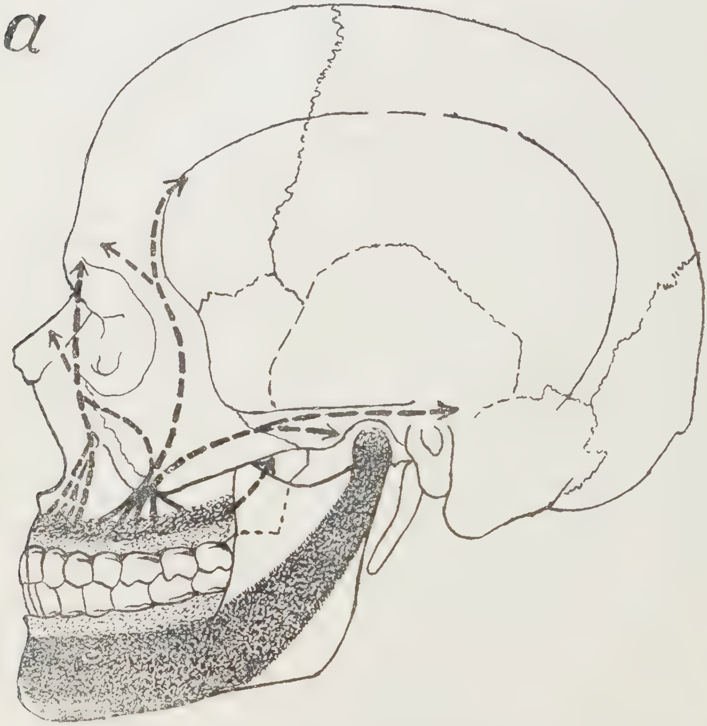

Fig. 144. *Homo sapiens* L. Adult skull showing the two basal arches (darkly dotted) and the facial pillar ('Gesichtspfeiler') (hatched). *a*. Right sight of the skull seen from the right side inverted.

With Marinelli (1936, pp. 230/231) we shall then distinguish in the higher Vertebrata, as the most important consequences of the suspension of the new upper jaw for the structure of the cerebral skull, the crista frontalis externa ("Stirnscheitelkante"), the orbital ring, and the temporal region (the region of the cheeks) with the zygomatic arches (see f.i. my figs 112, 113 *b*). The crista frontalis externa ("Stirnscheitelkante") acts as a buttress between the region of the praemaxillare and the place of origin of the chewing-muscles. The orbital ring attaches the maxillare to the crista frontalis externa ("Stirnscheitelkante") or to the temporal region. The temporal region, or its remains in the shape of zygo-

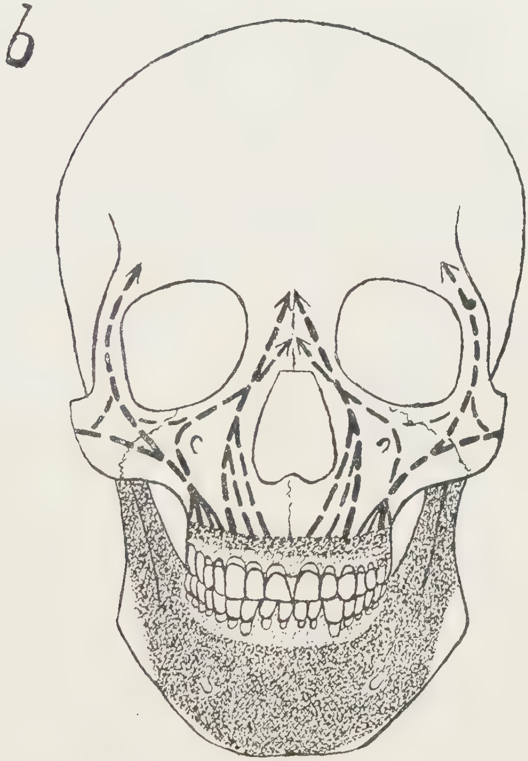

Fig. 144. *b*. Skull seen in front. After Bluntschli (1936), figs 4 b, 5 b.

matic arches are regarded by MARINELLI (1929, p. 132; 1933, p. 203; 1936, pp. 230/231) as the main element of a bridge-like construction, resting on two piers. The front pier is formed by the places of attachment of the upper jaw (as bearer of the centres of pressure in biting and chewing). The back pier is formed by the jaw joint. The chewing-muscle, originating from the zygomatic arch represents the load on the bridge.

This front pier is pierced by the orbita so that a construction is necessary to avoid loading it ("Umgehungskonstruktion", WETZEL); in this way the eye is kept free from pressure (MARINELLI, 1929, p. 135). Therefore we must distinguish a preorbital and a postorbital buttress ("Anlehnung") in the front pier. A firm attachment of the preorbital part of the new upper jaw to the firmly constructed, medially situated roof of the skull occurs along the rostral edge of the orbita and not along the ventral edge of the orbita, which, indeed, is often lacking and in other cases slightly developed. In the processes of the old upper jaw towards the base and sides of the neurocranium which will be discussed later on, we distinguish preorbital and postorbital connections (STADTMÜLLER, 1936, p. 569). All this fits in with the opinion that the orbita is a component of the skull with a well-nigh absolutely individual shape and size ("Eigenraum") which only allows of a firm attachment in front of or behind the orbita, so that the suspensorial mechanism of the new upper jaw and the places of attachment of the old upper jaw depend on the size of the orbita and its position in the skull.

In treating the suspensorial mechanism of the old upper jaw in Elasmobranchii the principal points will be 1° the suspension to the contralateral element or to the ethmoidal region, 2° the processus ethmoidalis and the processus orbitalis, 3° the development of the neurocranium on the spots where these processus are attached to it.

In the discussion of the suspensorial mechanism of the new upper jaw in higher Pisces it is mainly the far rostral point of attachment, which must be considered, because at the caudal end of the new upper jaw the suspension is very loose, or even entirely lacking. This far rostral suspension occurs directly to other covering bones of the snout, and via the ethmoidal region of the neurocranium indirectly to covering bones of the snout, and via this ethmoidal region also to the palatinum via the vomer and through the palatinum to the elements of the old upper jaw.

In Amphibia and Amniota, the praemaxillare too, is fastened to the palatinum and, consequently, to the old upper jaw, by means of the ethmoidal region and the vomeres. In the second place the back part of the maxillare is, in a number of Non-Mammalia, attached to the quadratum, via the zygomatic arches, consequently it is also attached to the old upper jaw. In the third place maxillare and praemaxillare are, in a number of groups, attached to the old upper jaw in still another way, *viz.* where a secondary palate occurs, because in that case a plate-shaped extension of the praemaxillare and certainly of the maxillare are connected with plate-shaped extensions of the palatinum and sometimes also of the entopterygoid, so with elements of the old upper jaw. A fourth manner of attachment occurs in some isolated groups where the maxillare is attached to the entopterygoid by means of the ectopterygoid or the os transversum, so to the old upper jaw.

Consequently the suspension of the old upper jaw to the neurocranium, is of importance to our subject. For our purpose the attachment of the pars palatina, the basipterygoid connection and the processus ascendens and the structures the cerebral skull makes with them, are of importance. Among these preorbital and postorbital connections are distinguished (STADTMÜLLER, 1936, p. 569); the places of these processes may, however, sometimes vary; nevertheless they are homologized by a number of authors. The most caudal postorbital connections and processes of the old upper jaw, such as the processus oticus, will be treated in the discussion of the suspension of the jaw joint. – The preorbital and postorbital connections between the old upper jaw and the neurocranium just mentioned, are all chondrocranial connections. If these connections are very powerful they are ossified, at the same time they may be strengthened by covering bones, such as the dermopalatinum and the entopterygoid. A very powerful suspension of the old upper jaw by means of the processus basipterygoideus or direct to the sphenoid is combined with a powerful structure of the skull base and even also of the squamosum (MARINELLI, 1929, pp. 131, 132; 1933, pp. 207, 213).

Three of the four ways of suspension of the new upper jaw via the old upper jaw to the cerebral skull discussed above (via the ethmoidal region and the vomer, via a secondary palate, via an ectopterygoid or an os transversum) may together be called the medial suspension of the new upper jaw. Hereto belongs MARI-

NELLI's so-called inward buttress ("innere Strebe") (1933, pp. 207, 213).

By the side of these we must distinguish the lateral buttress ("laterale Verstrebung") or the outward buttress ("aüssere Anlehnung") (MARINELLI, 1933, pp. 207/208). The latter is, in general, much more important for the suspension. When treating this, the material point is in the first place the preorbital and in the second the postorbital part of the front pier; in the third place the zygomatic arches. In the preorbital part of the front pier the principal point will especially be the attachment of that part of the new upper jaw to the ethmoidal region and to the covering bones of the snout, among which are the preorbital part of the orbital ring. For Mammalia we shall discuss separately the constructions connected with the parts of the new upper jaw bearing the incisivi, those bearing the canini and those bearing the praemolares. The second cardinal point is the front part of the postorbital region formed by the postorbital part of the front pier of the bridge-like construction; in this part occur the postorbital part of the orbital ring, in other groups the postorbital bar, which, however, in other cases has a different function [1]). The third principal point are the zygomatic arches as far as they are important for the attachment of the new upper jaw. The bridge of the nose, the crista frontalis externa ("Stirnscheitelkante"), as a matter of fact the entire median of the roof of the skull, the temporal region as far as the occipital region are, in a further connection, important for the attachment of the new upper jaw on the lateral side.

In treating the suspension of the new upper jaw in the manner indicated above, we commit two mistakes, which cannot be avoided, because something is separated which is inseparable. On the one hand we run the danger of treating questions which are not only relevant to the suspension of the new upper jaw, on the other hand we treat too little, as other matters are relevant to the suspension as well. To illustrate the former drawback we point out the postorbital bar which does not only serve to suspend the new upper jaw as we shall see in the following; secondly we point out the zygomatic arches which also serve for the attachment of the chewing-muscles and at the same time help the suspension of the back pier, that of the jaw joint. And as regards the second drawback we point out the fact that we shall, it is true, treat the most caudal part of the suspensorial mechanism with that of the jaw joint, but that this latter suspensorial mechanism may just as well serve the attachment of the upper jaw. We shall, *e.g.* treat the suspension of the pars quadrata of the palatoquadratum of Elasmobranchii in treating the suspension of the jaw joint, but it serves just as well to suspend the front part of the palatoquadratum, so of the dental plate because the dental plate and the jaw joint are parts of one and the same skeletal element. If, all this notwithstanding, we want to discuss the suspensorial mechanism of the upper jaw apart from the suspension of the jaw joint and the attachment of the chewing-muscles, this leads to difficulties which we want to state here at once.

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[1]) On the maxillary tuber in Mammalia, see: W. MONTAGUE COBB (1943), Amer. J. Anat. **72**, pp. 39–105. (Postwar addition in the manuscript)

b. The size of the suspensorial mechanism of the upper jaw

As we saw in the above the suspensorial mechanism of the upper jaw is very intricate because it consists of many elements, processes *etc.*, so that only an indication of the size of each of these elements would be reasonable.

The absolute size of the suspensorial mechanism of the upper jaw

I have not been able to find exact data on the absolute size of the suspensorial mechanism of the upper jaw in the literature I consulted.

In general we may say that large animals will have a large suspensorial mechanism of the upper jaw. The size indeed, depends on the force of the chewing-pressure, which is expressed in the development of the upper jaw and the size of the teeth, all these factors are connected with the size of the animal. But there is not only a connection with the size of the animal. There is also a connection with the way in which the food is seized, the way it is mastered, the chopping up of the food, – so with the kind of food, – the distribution of the chewing-pressure, – so the use of the teeth, – the caudal extension of the series of teeth or back teeth, a.s.o.

The relative size of the suspensorial mechanism of the upper jaw

Exact data on the relative size of the suspensorial mechanism or its elements were not to be found in the literature I consulted either.

Here, too, we can in general conclude that there is a connection with the relative size of the upper jaw and the teeth and so with the use of the teeth in seizing the food and chopping it up, so with the chewing-pressure and its distribution, and with the character of the food.

In stages of development

Relevant to our subject are those cases where the demands made on the suspension of the upper jaw are altered in the course of ontogeny, so that, in connection with this size and shape of the suspensorial mechanism are altered too.

Thus we find in the larvae of Amphibia, that the trabeculae serve as a buttress ("Widerlager") for the jaw apparatus, in this instance the old upper jaw. During this period the trabeculae are thick and powerfully constructed, later on they are partly resorbed (Stadtmüller, 1936, pp. 542/543). This is connected with the shifting of the position of the palatoquadratum in the ontogeny of Amphibia, which is caused by the growth of the lower jaw, in the development of the musculature of the chewing-apparatus *etc.* (Stadtmüller, 1936, p. 590) (see my fig. 145).

In adult animals

The discussion of the relative size of the suspensorial mechanism of the upper jaw can best be divided into three parts: in Elasmobranchii, in the higher Pisces and in Amphibia and Amniota. In Elasmobranchii the palatoquadratum is the functioning upper jaw, in the higher Pisces it is the praemaxillare with the maxillare, but this new upper jaw is not strongly attached to the skull, caudally, at any rate not by means of a zygomatic arch, while in Amphibia and Amniota the new upper jaw is suspended caudally as well, a.o. by means of zygomatic arches.

In Elasmobranchii

In most Elasmobranchii the rostral end of the palatoquadratum is connected with the contralateral element and not with the ethmoidal region. This latter is the case with the rostral end of the palatoquadratum of Holocephali.

The size of the processus ethmoidalis in certain Elasmobranchii and that of the processus orbitalis ("Orbitalfortsatz") in other

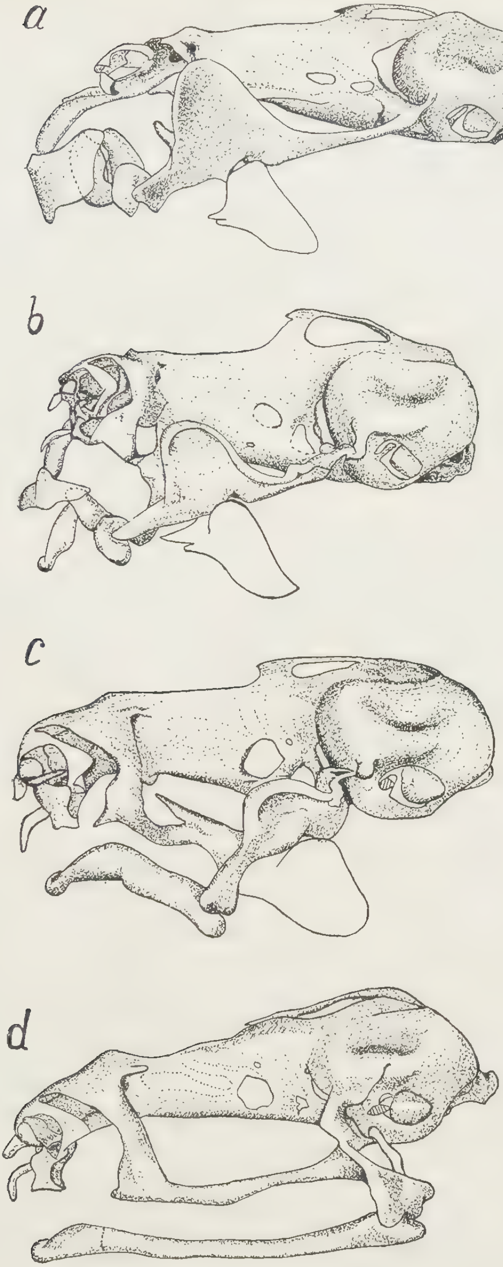


Fig. 145. *Rana* sp. Chondrocrania seen from the left side. *a*. Fully developed larval condition. *b*. and *c*. Intermediate stages. *d*. Adult. After G. R. de Beer (1937), pl. 75.

Elasmobranchii always remains relatively small (see my figs 61, 62).

As we mentioned above, the neurocranium in Elasmobranchii has, according to Marinelli (1936, pp. 230/231), changed very little under the influence of this suspensorial mechanism, because the dental plate, the place of attachment of the chewing-muscles and the jaw joint are all three situated on the palatoquadratum. All the same, we find here and there, a relatively strong development of the processus praeorbitalis and postorbitalis, which must be mentioned in this connection.

In higher Pisces

The higher Pisces will be discussed here separately because of the following reason: the new upper jaw is not strongly attached to the skull caudally, at any rate not by means of a zygomatic arch.

The medial suspension in higher Pisces

The medial suspension of the new upper jaw is brought about by the attachment by means of the primary upper jaw to the ethmo-vomer block, a joint lying between the block mentioned and the palatinum (Gregory, 1933, p. 414).

In many cases the new upper jaw is only slightly developed, as is also the primary upper jaw, so that the processes for the suspension of the primary upper jaw are small, or even entirely lacking, as are the processes of those parts of the neurocranium to which they are attached.

In other cases, however, the primary upper jaw is very powerful, a.o. in connection with the fact that it bears strong teeth on certain of its elements, in which case the suspensorial mechanism of this primary upper jaw to the neurocranium is strongly developed as well. In this connection we mention the picture of *Roccus lineatus* (Bl.) (Gregory, 1933, fig. 119) (see my fig. 19).

In certain cases the new upper jaw itself is big and powerfully constructed and in connection with this, its median suspension is big and powerful as well. Of the Sparidae, with their very powerful set of teeth, massive praemaxillare and great enlargement of the maxillare, Gregory (1933, p. 438, also p. 249, fig. 123) (see my fig. 89) mentions that the ethmo-vomer block shows equally great massiveness and strength and that the palatinum and its immense overlapping process shows a great enlargement, that the palatinum in its turn is braced by the stout parethmoid and mesethmoid and that also the parasphenoid is powerfully constructed.

In *Istiophorus* where the new upper jaw has developed into a very long snout, this is braced especially by the broad anterior end of the vomer joined by the well developed parasphenoid (GREGORY, 1933, p. 317, fig. 197 A).

The lateral suspension in higher Pisces

In front of the orbita the lateral suspension occurs as a suspension to other elements of the snout and to the ethmoidal region.

This suspension to the snout and to the ethmoidal region is sometimes lacking, as *e.g.* in *Polyodon spathula* (Walb.) (*Polyodon folium*) (GREGORY, 1933, fig. 17), and in *Acipenser* (figs 19 A, 20) (see my fig. 74), where the new upper jaw is only suspended to the primary upper jaw.

Where this preorbital suspension does occur, it is brought about by means of rostralia, nasalia, certain preorbital elements of the orbital ring *etc.*, and directly or, via the covering bones mentioned also indirectly, to the ethmoidal region of the primordial neurocranium. Sometimes this suspension is weakly developed as *e.g.* in Lyomeri such as *Gastrostomus*, where the exceptionally long new upper jaw is joined to a remarkably short and wide neurocranium, *i.e.* according to the picture, to the covering bones of the snout (GREGORY, 1933, p. 438, fig. 94) (see my fig. 87). In other cases the suspension is strongly developed. Thus, in *Istiophorus* the new upper jaw, which has developed into a very long snout, is especially braced by the broad nasalia (GREGORY, 1933, p. 317, fig. 197 B). In Sparidae with their great enlargement of the maxillare, we find a great strength of the interorbital bridge and of the cranial vault (p. 438) (see my fig. 89). For the rest we may remind the reader of the remark from GREGORY, cited above (1933, p. 286) that the suspension of the new upper jaw in *Balistes*, as in all other Vertebrata, makes its influence felt as far as the occipital region.

Special mention should be made of the suspension of the praemaxillare by means of an ascending process of this element of the new upper jaw. We find this when a protrusility of the mouth occurs, such as in Cyprinidae, Percoidei and Zeoidei (GREGORY, 1933, p. 424). In Cyprinidae the ascending processes of the praemaxillaria are attached to a "rostral bone", or "preëthmoid bone" which in turn is attached posteriorly to the anterior end of the mesethmoid (p. 189). In Percoidei the top of the ascending process of right and left praemaxillare and of the rostral cartilage situated below it, is flanked by a notch formed by the nasalia and upper part of the mesethmoid; a marked protrusion of the praemaxillare can only take place when the ascending process of the praemaxillare is greatly prolonged (GREGORY, 1933, pp. 239, 242) (see my figs 19, 21, 78, 81, 89, 115, 127, 128, 129). In Labridae, as in *Tautogolabrus*, *Lachnolaimus* and *Epibulus*, the ascending processes of the praemaxillaria are longer than the alveolar branch (GREGORY, 1933, pp. 256, 257, figs 129, 130, 131) (see my figs 81, 129). In *Zeus* with its protrusile mouth the elongate prefrontal-vomerine region serves for the support of the long ascending processes of the praemaxillaria (GREGORY, 1933, p. 271, fig. 148).

But also in other cases where there can be no question of protrusility of the mouth, we find such an ascending process of the praemaxillare. This lies against the elements of the snout, such as the dermethmoid, nasale, frontale *etc.* There are even cases where such an ascending process has no direct contact with a more dorsally situated element of the cranial roof, but remains at a considerable distance of it, such as is, according to the pictures the case with *Stylophorus chordatus* Shaw (fig. 176), *Periophthalmus* (fig. 228) (see my fig. 41) and *Callionymus* (fig. 242) (GREGORY, 1933).

Caudal of the orbita the development of the lateral suspensorial mechanism may differ widely. It is most closely connected with the caudal extension of the new upper jaw with regard to the orbita. When discussing the position of the new upper jaw with regard to the orbita, we saw that the caudal end of the new upper jaw may lie rostral of the orbita or ventral, but that it may also extend caudal of the back edge of the orbita. In this latter case only a postorbital suspension of the new upper jaw is possible, which may then be brought about by the caudal elements of the orbital ring and by the elements of the temporal region.

A suspension of the caudal part of a new upper jaw extending so far caudalward, to postorbital elements of the orbital ring is found in a number of pictures given by GREGORY (1933). I only want to mention the pictures of a number of † Palaeoniscidae (GREGORY, 1933, fig. 12) (see my figs 95, 143 *a*).

A suspension of the caudal part of such a new upper jaw to the temporal region is depicted for *Polypterus* (GREGORY, 1933, fig. 10).

In a number of cases the attachment of the caudal part of the new upper jaw to the cerebral skull is lacking. For examples of this we need only point to the phenomenon, exhaustively discussed before, that the caudal extremity of the new upper jaw crosses the lower jaw rostral of the quadratum-articulare joint, so that this caudal extremity comes to be situated lateral of the lower jaw. For examples we refer to this discussion. In some few cases a picture in GREGORY (1933) shows this caudal extremity as entirely loose in the lateral view, and it even does not cross the lower jaw, as is *e.g.* the case in *Holocentrus ascensionis* (Osbeck) (fig. 112), *Fierasfer* (fig. 257) (see my fig. 146), and *Lasiognathus* (fig. 275).

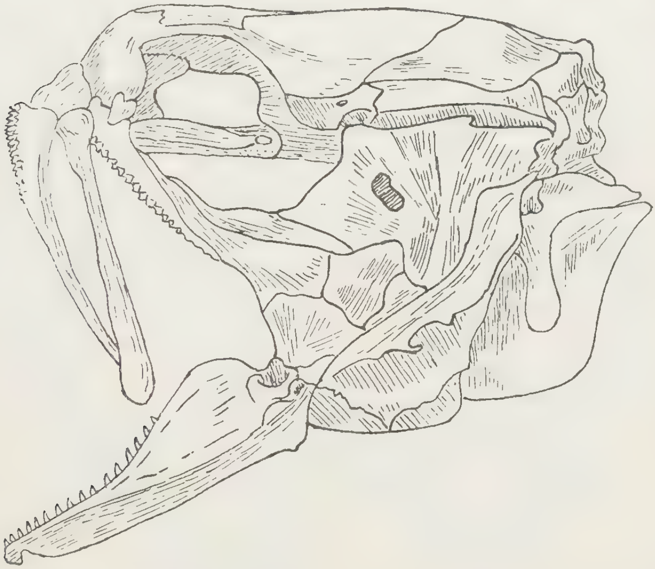


Fig. 146. *Fierasfer acus* (Brünn.). Skull seen from the left side. After GREGORY (1933), fig. 257 on p. 378.

In Amphibia and Amniota

In these higher Vertebrata the new upper jaw is suspended caudally, *viz.* by means of the zygomatic arches.

As stated in the introduction to this chapter, we shall successively treat the medial, and the different parts of the lateral suspension.

The medial suspension in Amphibia and Amniota

The three ways of medial suspension of the new upper jaw, mentioned in the introduction to this chapter, *viz.* those via the old upper jaw to the cerebral skull, do not always occur. Suspension by means of a secondary roof of the mouth, does not always occur, because in Amphibia, Sauria, Serpentes, Aves *etc.* there is no secondary roof of the mouth. The suspension via an ectopterygoid or os transversum, as occurs in Loricata, is comparatively rare. The suspension via the ethmoidal region and the vomer to the old upper jaw, does not always occur either, because sometimes the pars palatina of the palatoquadratum is reduced, as is the case in Caudata *etc.* Where in such forms both the secondary palate and an os transversum are lacking too, the new upper jaw is not suspended to the neurocranium by means of the primary upper jaw.

As a rule, however, the suspension of the new upper jaw by means of ethmoidal region and vomeres to the old upper jaw, is developed. The development and size of the processes of the old upper jaw serving for the suspension to the neurocranium depend very much on the mechanical demands made on the jaw. The demands made on the jaw and those made on its suspension, will, in general, run parallel (Versluys, 1936, pp. 717, 789/790).

When a slight development of the new upper jaw is combined with a simple, primitive set of teeth suitable to catch mobile prey, we find a weak development of the suspensorial apparatus and of the primary upper jaw. The attachment of the pars palatina to the ethmoidal region and the basipterygoid connection are weakly developed. This is the case in those Amphibia where the pars palatina is continuously cartilaginously connected with the ethmoidal region, but the basipterygoid connection is a loose one. In Sauria, Serpentes and Aves these two connections are movable because of the kinesis of these skulls. Yet in *Varanus*, *e.g.* where the maxillare is connected with the basisphenoid by means of the palatinum and the pterygoid, the processus basipterygoidei are very powerful, as is also the base of the skull itself (Marinelli, 1929, p. 132) (see my fig. 9).

With a more powerful development of the new upper jaw, as is found in many marine Reptilia, and in Reptilia living on land and hunting big prey, where we find, consequently, a specialized set of teeth, and especially also with the powerful development of the new upper jaw, as is found in Mammalia with a set of teeth

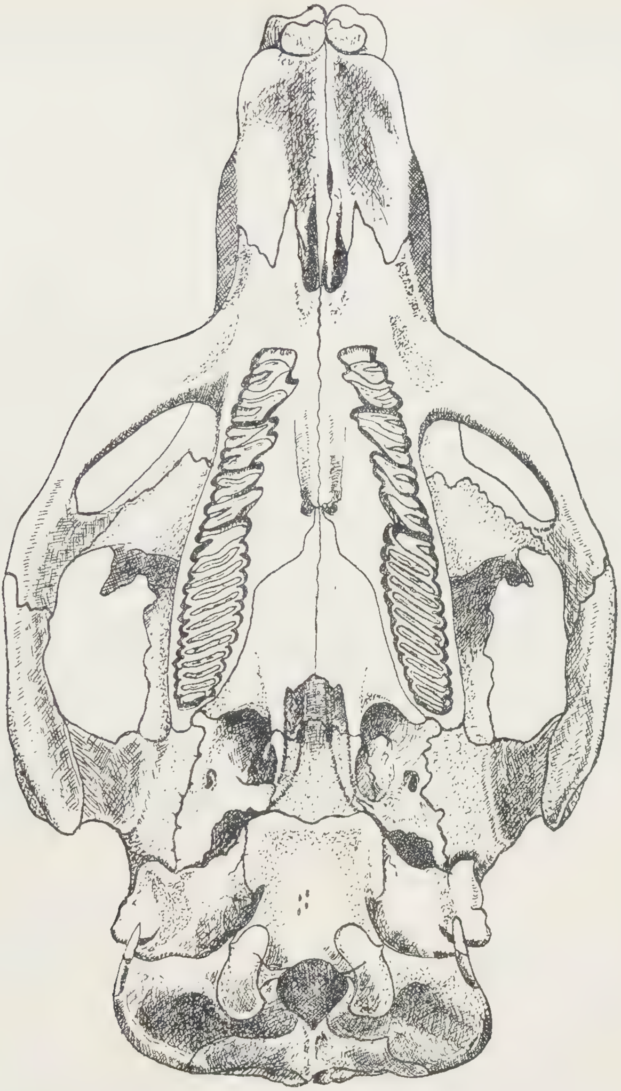


Fig. 147. *Hydrochoerus hydrochaeris* (L.) (*Hydrochoerus capybara* Erxl.). Skull seen in ventral view. After WEBER (1927), I, fig. 40 on p. 60.

specialized for chewing, the medial suspension of the new upper jaw by means of the old upper jaw, is very powerfully developed. This condition is combined with akinesis (VERSLUYS, 1936, pp.

741, 741/742, 742, 747). The connection between the palatinum and the ethmoidal region is broad and at the same time immovable. The basipterygoid connection is also broad and immovable. In *Chelonia* the connection in the ventral median is very strongly developed, because here left and right entopterygoid lie against each other along a considerable distance. In Mammalia the so-called inner buttress ("innere Strebe") is, according to MARINELLI (1933, pp. 207, 213) formed by the teeth-bearing part of the maxillare, the palatinum, the pterygoid process of the basisphenoid, the alisphenoid and the squamosum (see my figs 107 *c*, 110 *c*, 147). Where the musculus pterygoideus plays an important part, the back-teeth are situated somewhat more below this inner buttress ("innere Anlehnung") (MARINELLI, 1933, pp. 207/208). This inner buttress ("innere Strebe") is not equally strongly developed in all Mammalia. According to MARINELLI (1929, p. 131) the attachment of the maxillare by means of the palatinum to the lateral wings of the os sphenoideum is stout in *Camelus* and *Cervus*, but weak in *Bos*. In *Giraffa camelopardalis* (L.) the inner buttress ("innere Strebe") is not very considerable either (MARINELLI, 1933, p. 208).

In these cases of stout medial suspension of the new upper jaw in these akinetic skulls, this suspension is reinforced by the secondary palate, where laminary extensions of the praemaxillare, and in any case of the maxillare are over a great length connected with laminary extensions of the palatinum, as occurs in Testudinides, Loricata and Mammalia. In Loricata this connection is again reinforced because the entopterygoid forms a laminary extension in the secondary palate, caudal of that of the palatinum.

An accessory suspension occurs when the maxillare is suspended to the entopterygoid, and, consequently to the old upper jaw, by means of the ectopterygoid or os transversum, as occurs in Loricata.

The influence of this suspension of the new upper jaw by means of the old upper jaw is further apparent in the size and development of the ethmoidal region and of the base of the skull, and from there as far as the occipital region.

The processus ascendens of the palatoquadratum or the epipterygoid extending upward to the roof of the skull, may also be said to belong to the medial suspension. This process is not always present. In *Varanus* it is a thin rod (see my fig. 9). In

Sphenodon the epipterygoid is more powerfully developed. If the alisphenoid of Mammalia is homologous with the epipterygoid, this well developed element forms an important part of the medial suspension, as we saw above.

The lateral suspension in Amphibia and Amniota

The lateral buttress ("laterale Verstrebung") is much more important for the suspension of the new upper jaw than the medial one (Marinelli, 1933, p. 208). For through this the new upper jaw is attached to the very powerful medial part of the roof of the skull, or its roof in general, and even further to the occipital region, by means of the sides of the facial skull. Marinelli (1929, pp. 130, 131, 132) mentions this for *Varanus* (see my fig. 9), *Camelus* and *Bos*. Especially in cases where the musculus masseter plays an important part, and where the upper teeth are pressed outward by a scissor function of the teeth ("scherende Gebisswirkung") we see the back-teeth situated more under the strongly developed outward buttress ("aüssere Anlehnung") (Marinelli, 1933, pp. 207/208).

As we mentioned in the introduction to this chapter, we shall separately treat the different elements of the lateral suspension, first the preorbital part of the front pier, divided again in Mammalia according to the structures connected with the incisivi, with the canini and with the praemolares; then the postorbital part of the front pier (postorbital part of the orbital ring, postorbital bar) and, finally, the zygomatic arches.

The preorbital part of the front pier in Amphibia and Amniota

Size and development of this preorbital part of the front pier of the suspension of the new upper jaw, are connected with the size of the praemaxillare and of the front part of the maxillare, which in its turn is connected with the development and the size of the teeth. This depends on the function of the teeth in seizing and chopping up the food, the strength of the chewing-pressure and its distribution. Ultimately this is connected with the size of the animal and the character of the food.

In recent Amphibia this preorbital part of the lateral suspension is weakly developed, with a few exceptions, as f.i. Gymnophiona (see my figs 31, 96). Among † Stegocephala a powerfully developed preorbital part of the lateral suspension may occur (see my figs 38, 39).

In *Varanus* the pressure exercised on the teeth of the new upper jaw, also that upon the most caudal teeth (the series of teeth ends at the front edge of the orbita) is borne entirely by the preorbital part of the front pier, transmitted along the front of the orbita to the roof of the forehead and from there farther on (Marinelli, 1929, p. 135) (see my fig. 9). A similar condition is found in other groups as well (see my fig. 44).

In Reptilia with a powerfully developed, big new upper jaw, the preorbital part of the lateral suspension is powerfully developed too, as is the case in Testudinides, Loricata *etc.* (see my figs 53, 54, 55, 100, 101, 102, 103).

In Aves, especially in those where the bill is a weakly developed pincer, the preorbital suspension is weakly developed as well (see my figs 14, 36, 57, 98; see also my figs 15, 34, 52, 56, 69, 106).

In Mammalia we shall, in view of Marinelli's data, divide the discussion of the preorbital suspension in the constructions connected with the incisivi, with the canini and with the praemolares.

The influence of the incisivi on the development of the preorbital part of the front pier of the lateral suspension of the new upper jaw is very great and strongly dependent on the presence or absence of incisivi and their size.

In *Lepus* ("hare") the upper incisivi are, according to Marinelli (1929, p. 133) (see my fig. 111), pushed upward and forward by the lower incisivi in gnawing. The upper incisivi are firmly attached to the rest of the skull along two ways: first by means of the processus frontalis ossis praemaxillaris to the roof of the skull, and secondly by a bony bridge in the plane of the palate with the part of the maxillare bearing the molares; between these two bony connections the bone has disappeared.

In *Equus caballus* L. we find a construction similar to that in *Lepus*, *viz.* a processus frontalis ossis praemaxillaris (Marinelli, 1929, p. 133; 1933, pp. 211, 212) (see my fig. 149). In *Lepus* and in *Equus caballus* L. the set of teeth consists of two clearly divided parts, so that we can more easily analyse the constructive principles in the skull which either of these parts must fulfill, than in cases, where the two parts are continuous, as in Carnivora (Marinelli, 1933, p. 211). Such a construction, due to two clearly divided parts of the set of teeth, also occurs in other cases (see my figs 26 and also 60).

In *Giraffa camelopardalis* (L.) the lack of the upper incisivi in the long front part of the new upper jaw entails that no chewing-pressure is transmitted in front of the ridge on the curved edge of the lacrimale, as may be seen from the size of the facial part of the lacrimale, from holes in the wall of the skull in that region *etc.* (MARINELLI, 1933, pp. 206, 208) (see my fig. 150). A similar condition occurs in other Ruminantia (see my figs 37, 99, 112).

The influence of the caninus on the development of the preorbital part of the front pier is extremely great, as may be established when the caninus is absent, or with canini of different sizes. The development of the caninus determines the direction of the sutures between maxillare and frontale and the structure of this small region, but it also determines the profile of this part of the skull, and consequently, that of the entire skull (MARINELLI, 1929, p. 139).

The root of a strongly developed caninus extends into a processus frontalis of the maxillare, this processus transmits the pressure to the frontale and farther (MARINELLI, 1929, pp. 137, 139). Perpendicular to this line of pressure we find a suture between the processus frontalis of the maxillare and the frontale. This condition is found in Carnivora, Traguloidea and *Dicotyles* (MARINELLI, 1929, pp. 137, 138). As MARINELLI (1929, p. 138) elaborates for *Panthera leo* (L.) the caninus must not only withstand a pressure in the direction of the longitudinal axis of this tooth, but also a backward pressure from the lower caninus, because, in biting, a backward pressure is exercised.

Curiously enough, *Moschus*, which has very long tusks ("Hauern") does not possess this sutural connection between maxillare and frontale, but the skull shows a hole in that spot, so that here there can be no question of a transmission of pressure of the muscles of the temporal region (MARINELLI, 1929, p. 138).

In all Suidae, where the upper canini are curved upward, maxillare and frontale are contiguous, but they lie side by side, not in a line (MARINELLI, 1929, p. 138) (see my figs 49, 71).

When the upper caninus is absent, the processus frontalis of the maxillare and the sutural connection described above, are lacking as well; we find, on the contrary, a hole where, in other cases, frontale and maxillare touch each other, as in *Lepus* (see my fig. 111), Cervidae, *Giraffa camelopardalis* (L.), or a very thin spot as in *Equus caballus* L. (MARINELLI, 1929, pp. 133, 137).

We saw that also the profile of the skull is influenced by the size of the caninus (see my fig. 148). According to MARINELLI (1929, p. 139) this is most obvious from the contrast between the profile of the skull of *Canis familiaris* L. and *Felis catus* L. MARINELLI elaborates this point in detail for the profiles of two Canidae, *Canis lupus* L. and *Cuon*. In *Canis lupus* L. the caninus is relatively

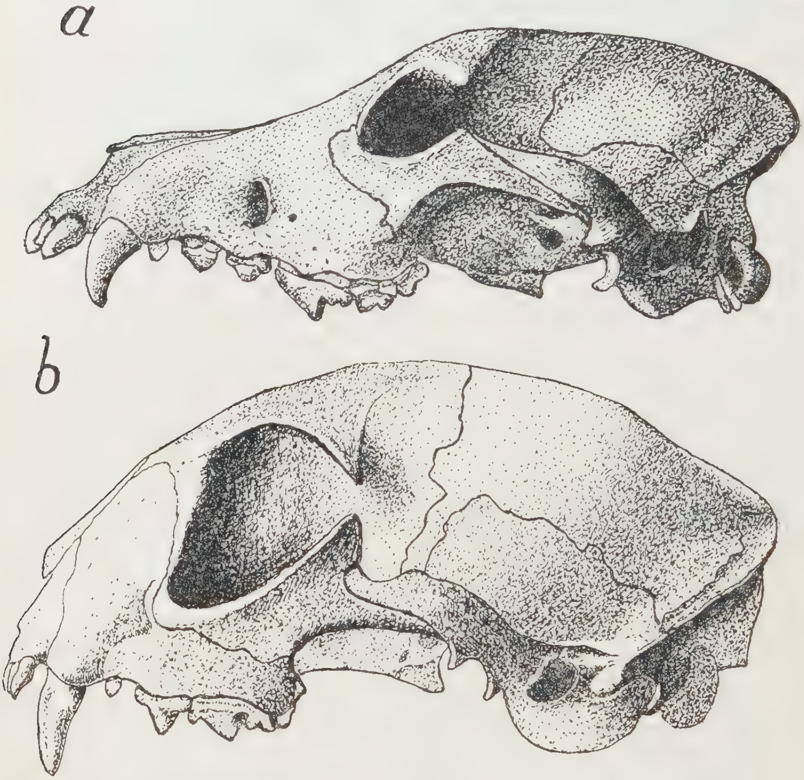


Fig. 148. *a. Canis lycaon* Schreber (*Canis lupus canadensis*). Right side of the skull seen from the right side inverted. *b. Felis catus* L. ferus. Skull seen from the right side inverted. After DUCROTAY DE BLAINVILLE (1839–1864), Atlas Tome II, G. *Felis* Pl. IX and G. *Canis* Pl. VII. Both skulls are drawn to about the same premaxillon-basion length.

weak, which is connected with the way in which the prey is chased, and the caninus is planted in a prolonged snout which sags in front of the eyes, in the so-called glabella. In *Cuon* the caninus is relatively more strongly developed; the prey is bitten and not snapped at; consequently the glabella is missing and the line of the profile slopes steeply upward.

The influence of the praemolares on the development of the preorbital part of the lateral suspension of the new upper jaw, is very great as well.

By way of exception the preorbital part of the front pier not only buttresses the praemolares, but all the cheek teeth, also those not situated in front of the orbita. This is the case in *Hyaenodon* where the forward direction of the roots of the teeth indicates the direction of the chewing-pressure. In *Hyaenodon* evident fortifying ridges ("Versteifungsrippen") run from the roots of the molares to the front edge of the orbita. These ridges are lacking in "*Pluodon*" where the row of back-teeth reaches farther backward, and the backmost teeth are out of the reach of the support of the preorbital part of the front pier (Marinelli, 1929, p. 137) (see my fig. 154).

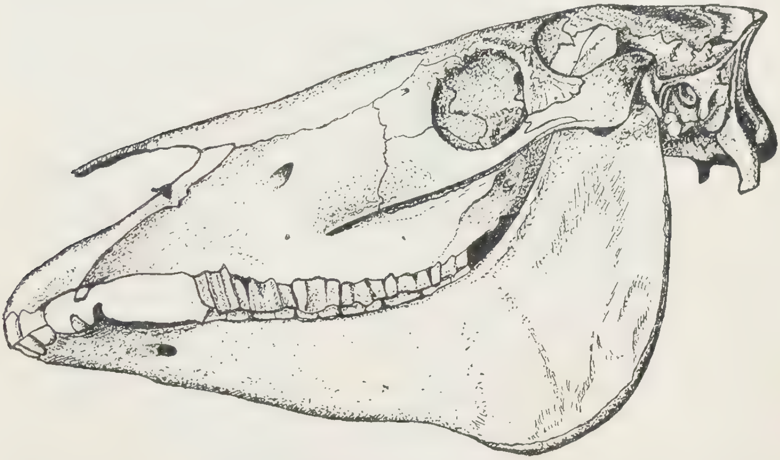


Fig. 149. *Equus caballus* L. 5 years old. Skull seen from the left side. After Martin (1914), fig. 106 on p. 120 b.

Of *Equus caballus* L. Marinelli emphatically mentions (1933, p. 212) (see my fig. 149) that the front part of the row of back-teeth is supported by the preorbital part of the front pier, in which the maxillare is firmly attached to the praemaxillare, nasale and frontale.

Perhaps the ridge on the curved edge of the lacrimale in *Gi-*

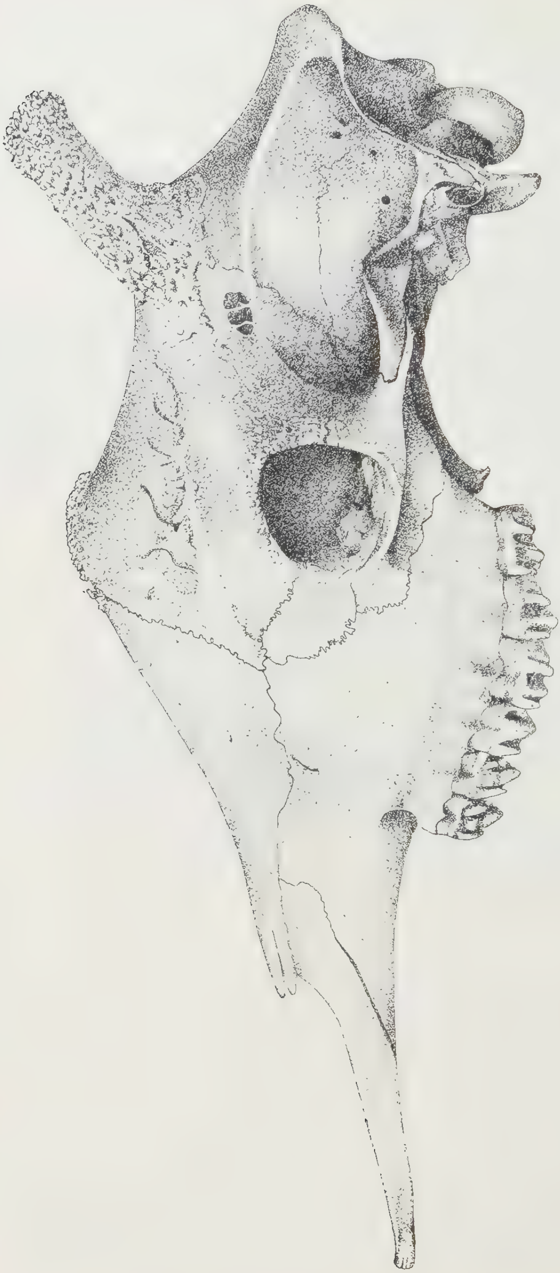


Fig. 150. *Giraffa camelopardalis* (L.) ♂. Skull seen from the left side. R.M.N.H. Leiden, no. 7085. 0.28×. Original drawing by G. W. M. Kurpershoek.

raffa camelopardalis (L.) which is continued in a ridge of the frontale above the orbita, may also serve as a support of the praemolares (MARINELLI, 1933, p. 206) (see my fig. 150).

To this we will add some remarks on the development of the lacrimale. MARINELLI (1929, p. 138) points out that the facial part of the lacrimale is very small or even almost entirely lacking in those cases where a line of pressure runs from the direction of the teeth to the forehead, passing in front of the eye (example Felinae and Primates); when, however, no such line is in evidence, the facial part of the lacrimale is large. From a passage in STADTMÜLLER (1936, pp. 980/981) it may be inferred that the development of the molares and the head-weapons of Artiodactyla, influence the size of the orbital and the facial part of the lacrimale.

The postorbital part of the front pier in Amphibia and Amniota

This consists of the postorbital part of the orbital ring, and the postorbital bar which suspend the caudal end of the maxillare.

An orbital ring which is closed postorbitally, attaching the caudal end of the maxillare to the temporal roof occurs in three Reptilia examined by MARINELLI, *viz. Sphenodon* (*Hatteria*), *Iguana* and *Hydrosaurus* (*Lophura*), in which the row of teeth extends backwards as far as below the orbita (MARINELLI, 1929, p. 135) (see my fig. 151). In *Varanus*, where the row of teeth stops at the front end of the orbita, no powerful caudal attachment of the maxillare is necessary, according to MARINELLI, and, consequently, the postorbital bar is weakly developed (see my fig. 9). MARINELLI also expresses it thus (1929, p. 135): in *Hydrosaurus* (*Lophura*) a buttress to withstand pressure ("Druckstrebe") runs from the caudal end of the maxillare obliquely upwards and backwards to the temporal roof; the front edge of this support forms the postorbital bar. In *Iguana* a bar runs perpendicularly from the upper zygomatic arch, the front edge of which is also the caudal limit of the orbita. A postorbital bar is also found in other Reptilia (see my figs 32, 54, 100, 101, 102).

In Aves the entire orbital ring has lost its significance as a buttress ("Widerlager") of the upper jaw, in connection with the other function of the jaw; we point to the fact that the more caudal parts of the bills of Aves are not used for biting, and that only the points are used for snatching (MARINELLI, 1936, p. 837).

A postorbital bar, whose function is the suspension of the new upper jaw, is found in certain Mammalia. Other functions of a postorbital bar are, according to MARINELLI (1933, p. 205) the attachment of the jaw joint, the formation of a firm base for horns and antlers, and finally a protection for the eye against pressure. These different functions will be discussed with the subjects concerned. We shall here discuss the importance of the postorbital bar for the attachment of the caudal end of the maxillare.

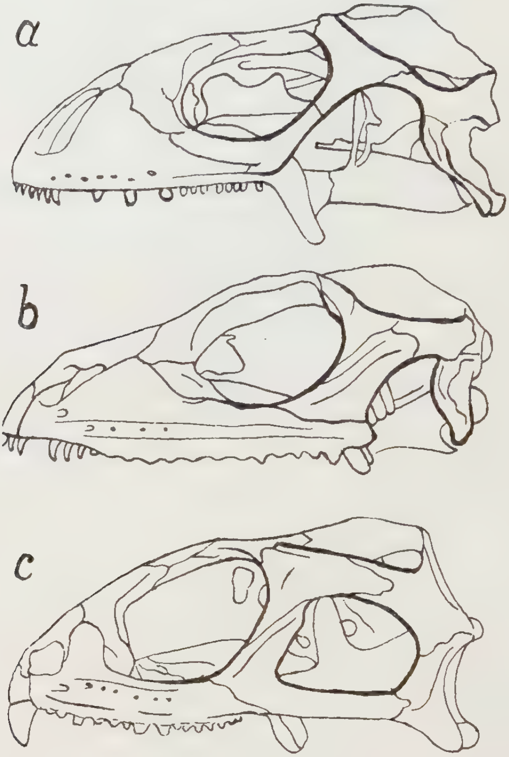


Fig. 151. Right side of skulls of Reptilia seen from the right side inverted. *a. Iguana. b. Hydrosaurus* (*Lophura*). *c. Sphenodon* (*Hatteria*). After MARINELLI (1929), figs 4, 5 and 6 on p. 134.

The development of the postorbital bar in *Giraffa camelopardalis* (L.) is discussed by MARINELLI as an example (1933, pp. 206/207, 208, 209, 210/211, 213/214, 215) (see my fig. 150). In *Giraffa camelopardalis* (L.) the chewing-pressure is directed obliquely outwards, the median strengthening given in the medial wall of the temporal groove, is less important than the lateral strengthening, wherein the zygomatic arches have become less important in comparison with the postorbital bar. The latter is heavily taxed by the chewing-muscles (musculus masseter and musculus temporalis) and forms the main buttress for the row of backteeth. Consequently the postorbital bar rises perpendicularly from the upper jaw immediately lateral from the back-teeth. That this and no other is the function of the postorbital bar in *Giraffa camelopardalis* (L.) is also apparent from its construction: its larger part is formed by the jugale, a small part of the bar by the frontale, while the squamosum is not involved.

The zygomatic arches in Amphibia and Amniota

The zygomatic arches also fulfill a task in the suspension of the new upper jaw, and especially in the suspension of the caudal end of the maxillare. The chewing-pressure exercised on the maxillare is transmitted to the zygomatic arches, and even farther (MARINELLI, 1933, p. 204). In addition to this, however, the system of zygomatic arches also has an important function as a place of attachment for the chewing-muscles. It is, of course, impossible to distinguish the constructive elements in the structure and position of the zygomatic arches according to these two functions. The zygomatic arches will be mainly treated in the discussion of the attachment of the chewing-muscles. Here we shall only enter into some aspects evidently connected with the suspension of the caudal end of the maxillare.

The development of the zygomatic arches and of the temporal region of the secondary roof of the skull in general, is most closely connected with the firmness and the manner of the attachment of the suspension of the new upper jaw, also with kinesis and akinesis (MARINELLI, 1936, p. 227; VERSLUYS, 1936, p. 717). And this is especially so with regard to the suspension of that part of the maxillare, which extends caudal of the orbita, with the extension of the teeth and back-teeth in that region and with the strength of the chewing-pressure on the spot.

Among the Reptilia examined by MARINELLI (1929, p. 135) (see my fig. 151) the row of teeth of *Sphenodon* (*Hatteria*), *Iguana* and *Hydrosaurus* (*Lophura*) extends backward as far as below the orbita, one upper zygomatic arch buttresses the attachment of the caudal end of the maxillare through the postorbital bar. In

Varanus, where the row of teeth ends at the front edge of the orbita already, the upper zygomatic arch, though present, does not play a part in the suspension of the maxillare (Marinelli, 1929, p. 135). The slight demands put to the jaws ("Inanspruchnahme") may be regarded as one of the causes of the gymnocrotaphy met with in Serpentes (Stadtmüller, 1936, p. 605) (see my figs 104, 105).

In most groups of Tetrapoda the lateral edge of the dentition ("laterale Zahnkante") behind the orbita would, according to Marinelli (1929, p. 136), find its buttress ("Anlehnung") in the zygomatic arch. It stands to reason that the role of the zygomatic arch in the suspension of the maxillare is very important in cases, where the row of molars extends as far as below the zygomatic arch.

In this connection there is a remarkable contrast between the carnivores and the herbivores among Mammalia. In Carnivora with an indistinct angulus mandibulae, where, consequently, the jaw joint lies on the same level as the chewing-plane, the chewing-pressure is greatest on the most backward molares. On the other hand, the chewing-pressure is equally distributed in herbivorous Mammalia with a distinct angulus mandibulae, where, consequently, the jaw joint lies at a higher level than the chewing-plane. In herbivorous Mammalia the back-molares are much less buttressed by the zygomatic arch than in Carnivora, because in herbivorous Mammalia the caudal end of the maxillare – and with it also the molares – lies much more medialward, below the medial wall of the temporal groove, perpendicularly under the middle part of the skull, *i.e.* the median high part of the skull. *Sus* is an example of this (Marinelli, 1929, p. 136) (see my fig. 152). In Carnivora where the chewing-pressure is greatest on the back-molares, the buttressing of these teeth by the zygomatic arch is developed to an extreme degree (Marinelli, 1933, p. 210). Here the rostral end of the zygomatic arch and so the musculus masseter ("Brechscherenmuskel"), the muscle for the scissor-function to break the food which is inserted on it, juts out laterally (see my fig. 153). This angle at which the zygomatic arch juts out, as well as the width of the curve of the zygomatic arch is stronger as the teeth are more powerful (Marinelli, 1929, p. 136). All this depends on the strength of the lateral pressure exercised upon the scissor-like mechanism ("Brechschere") when gripping the prey. In this connection Marinelli (1929, pp.

136/137) points to the differences between the conditions in Felinae, in *Canis* with its broad grinding-surface ("Mahlfläche") and in Pinnipedia with their reduced set of teeth. In Pinnipedia

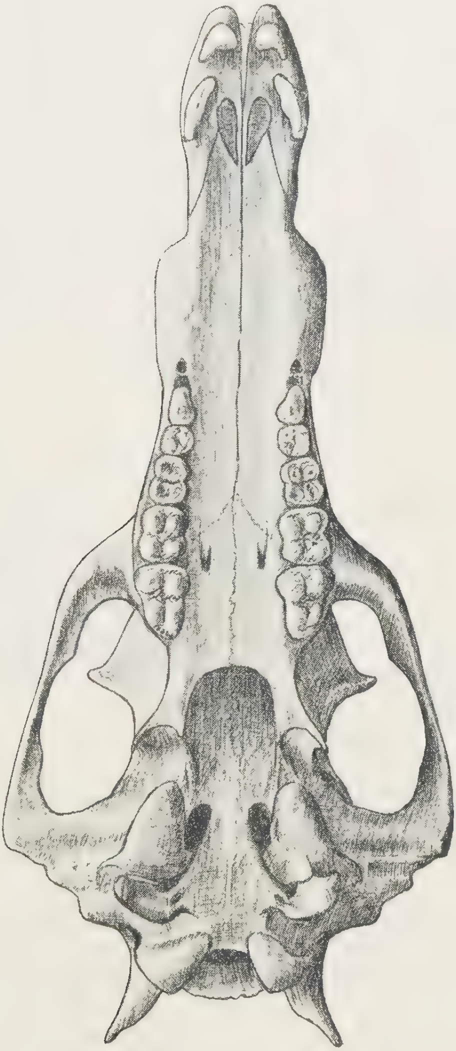


Fig. 152. *Babyrousa babyrussa* (L.). Skull seen in ventral view. Zool. Mus. Buitenzorg, no. 3293. 0.5×. Original drawing by Mrs M. IDENBURG in the collection of dr K. W. DAMMERMAN.

the zygomatic arch stands practically perpendicular on the side wall of the skull, and cannot take any pressure from the teeth (Marinelli, 1929, p. 137) (see my fig. 48). The reverse occurs in *Panthera leo* (L.), where it is however, clear that no transmission of pressure on the inner wall of the orbita takes place (Marinelli, 1929, p. 136). In Carnivora it is generally the zygomatic arch which buttresses the back-molares against chewing-pressure (Marinelli, 1933, p. 204). Very remarkable for the significance of the zygomatic arch for the attachment of the new upper jaw is what Marinelli observes about the difference between *Hyaenodon* and "*Pluodon*" (Marinelli, 1929, p. 137) (see my fig. 154). In *Hyaenodon* the maxillare is supported by the preorbital part of the front pier, consequently the zygomatic arch is practically

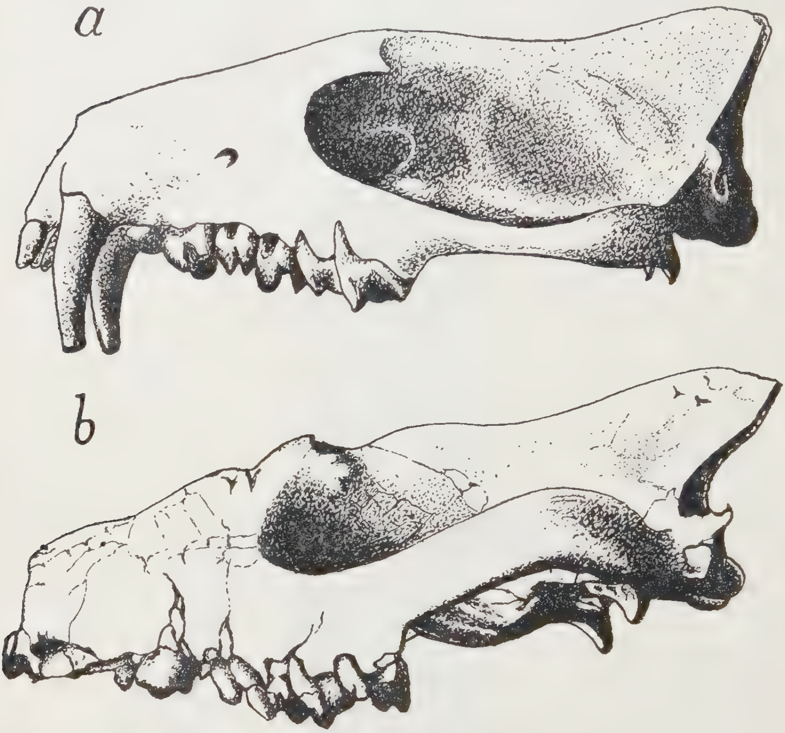


Fig. 154. *a. Hyaenodon cruentus* Leidy. Skull seen from the left side. After Marinelli (1929), pl. XII, fig. 12. *b.* '*Pluodon hyaenoides*'. Skull seen from the left side. After Marinelli (1929), pl. XIII, fig. 14. Both skulls are drawn to the same premaxillon-basion length.

straight. In "*Pluodon*" this does not hold good for the most backward molares, and, consequently, the zygomatic arch shows the upward curve, betraying adaptation to higher demands ("Inanspruchnahme") characteristic of Carnivora in general.

Besides of the influence of the chewing-pressure working in the direction of the longitudinal axis of the molares, we know still another influence of a different pressure on the molares and on the zygomatic arch. In † *Dinictis* and *Nimravus* (*Archaelurus*) (see my fig. 155) in biting a backward pressure was exercised on the lower jaw. This pressure was partly stemmed by the transversely placed last upper molar, which fits against a molar of the lower jaw; in connection with this the root of the zygomatic arch is not directed upwards but runs practically horizontally backwards, thus buttressing the caudal end of the new upper jaw against this particular pressure (MARINELLI, 1929, pp. 138/139).

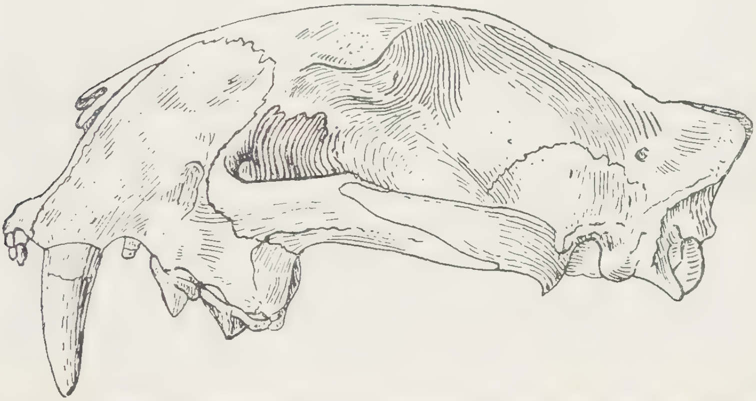


Fig. 155. *Nimravus gomphodus* Cope (*Archaelurus*). Skull seen from the left side 0.45×. After MATTHEW (1910), fig. 11 on p. 311.

c. The position of the suspensorial mechanism of the upper jaw

In the discussion of the suspensorial mechanism of the new upper jaw, topographical moments played a very important part. We only mention the subdivision into a front pier and the zygomatic arches; of the front pier into a preorbital part and a postorbital one; of the orbital ring into a preorbital and a postorbital part, *etc.* A discussion of the position of the suspensorial mechanism would, for the greater part, amount to a repetition of the information given above. So we shall limit ourselves to the following observations.

The processus orbitalis of the palatoquadratum ("Orbitalfortsatz") of certain Elasmobranchii protrudes into the orbita, generally in the back part, sometimes in the front one (Holmgren & Stensiö, 1936, pp. 318, 319, figs 238, 240; see also Marinelli, 1936, figs 198, 200 "processus ethmoidalis"). In other respects, too, the position of the processus orbitalis of certain Elasmobranchii is rather varying, also in relation to the processus ethmoidalis of other Elasmobranchii, which is considered homologous with the first-mentioned process by some authors.

The position of the basipterygoid connections of the higher Vertebrata is rather varying as well and certainly different from the place of more rostrally situated connections which are sometimes homologised with it.

About the position of the suspensorial mechanism of the upper jaw, it must yet be observed that with movable upper jaws and kinetic skulls the position of certain components of this mechanism is not always the same with regard to the upper jaw, or to other components of this mechanism or with regard to the rest of the skull.

d. Homology and non-homology

When judging the size and the position of the suspensorial mechanism of the upper jaw, it must be borne in mind that this suspensorial mechanism is certainly not formed by one certain morphological unit, but that very diverse parts play a role here and that we may have to deal with very different parts in different groups. So it is reasonable to put the question of homology or non-homology only with regard to well-defined components.

Thus it must be borne in mind when regarding the varying positions of the processus orbitalis in the orbita as are met with in Elasmobranchii, that, according to certain authors, non-homologous processes have been taken together under one name. In view of the diversity in position of the processus orbitalis in certain Elasmobranchii and of the processus ethmoidalis in other Elasmobranchii, it is important to know that these processes are not homologous according to some authors and homologous according to others, some of them even admit the possibility of their being homologous with the basipterygoid connection of the higher Vertebrates.

9. SUSPENSORIAL MECHANISM OF THE JAW JOINT

a. Introduction

Much of what has been said in the introduction to the discussion of the suspensorial mechanism of the upper jaw may be repeated here, because the same demands apply to the two suspensorial mechanisms.

It is necessary for the jaw joint to be immovably buttressed ("starr verstrebt") with regard to the origin of the chewing-muscles in order to make exertion of pressure in biting and chewing possible (Marinelli, 1936, pp. 230/231). Herein lies the significance of the skeletal connection between these two spots, as cartilage and especially bone can withstand pressure, as opposed to tendons and ligaments (Marinelli, 1929, p. 129).

The fact that, in Elasmobranchii, jaw joint and place of origin of the chewing-muscles are situated on one single piece of the skeleton, *viz.* the palatoquadratum, is, according to Marinelli (1936, pp. 230/231) the cause that the suspensorial mechanism of the jaw joint has only very slightly influenced the cerebral skull.

In higher Vertebrata, however, jaw joint and places of origin of the chewing-muscles lie on different elements of the skeleton and other skeleton elements have been intercalated between these two points (Marinelli, 1936, pp. 230/231). This has not only its consequences for the structure of the intermediate skeleton elements, but the pressure exercised on the jaw joint is transmitted on the rest of the skull, as far as the occipital region. In this connection we might repeat what was derived from Marinelli (1929, p. 128; 1936, pp. 230/231) and Gregory (1933, p. 286) in the preceding discussion of the suspensorial mechanism of the upper jaw.

Among these higher Vertebrata the construction of the suspensorial mechanism of the jaw joint of the higher Pisces is characterized by the importance of the hyomandibulare; this is not the case in Amphibia and Sauropsida, but the jaw joint is still a quadratum-articulare one, while in Mammalia the jaw joint is a squamosum-dentale one.

In the following discussion we shall deal with processes and other formations by which the part of the skeleton bearing the jaw joint (so the pars quadrata of the palatoquadratum, the quadratum, the squamosum) is suspended, as well as the formations meeting these processes *etc.* and which in their turn suspend the bearer of the jaw joint.

In Elasmobranchii we have to deal with the processes of the pars quadrata of the palatoquadratum, such as the processus oticus, the suspension of the pars quadrata, either by means of a processus oticus or not, to the hyomandibulare or (and) to the neurocranium itself, the size *etc.* of the hyomandibulare, the suspension of the hyomandibulare to the neurocranium, and the like.

In the higher Pisces we have to deal with the suspensorium, the development of the quadratum in this connection, symplecticum and metapterygoid, which both suspend the quadratum to the hyomandibulare, and the suspension of the hyomandibulare to the neurocranium.

In Amphibia and Sauropsida we have to deal with the extension of the quadratum, such as the processus oticus of the quadratum, the attachment to the processus paroticus, either by means of a rest of the hyomandibulare or directly, or the attachment directly to the neurocranium. Apart from this chondrocranial suspension we have also to deal with the suspension of the quadratum to the secondary roof of the skull, such as to the quadratojugale, squamosum *etc.* This latter attachment is connected with the development of the zygomatic arches and that of the temporal region of the secondary roof of the skull in general. Therefore the zygomatic arches themselves are of importance to us in the discussion of the suspension of the jaw joint.

In Mammalia we have, in our discussion, to deal with the squamosum which bears the fossa glenoidea, the attachment of the squamosum to the skull, the zygomatic arch, and, in some cases, the postorbital bar. The median high part of the skull plays an important part in the attachment of the jaw joint.

If we treat the suspensorial mechanism of the jaw joint in this way, we consider on the one hand too much, on the other too little. Too much because *e.g.* the suspension of the pars quadrata of the palatoquadratum of Elasmobranchii contributes at the same time to the suspension of the pars palatina. Too little, because, in Elasmobranchii, the suspension of the pars palatina also serves for the suspension of the pars quadrata. In the higher Pisces the metapterygoid serves for the suspension of the quadratum to the hyomandibulare, but, because the metapterygoid connects the upper part of the palato-pterygoid quadratum arch with the hyomandibulare (GREGORY, 1933, p. 414) it also contributes to the suspension of the palatinum, and so to that of the new upper jaw. We saw that MARINELLI regards the suspension of the jaw joint as the back pier of a bridge-like construction, the supporting part of which is formed by the zygomatic arch itself. So the zygomatic arch plays a part in the suspension of the jaw joint, but, as we saw, it also plays a part in the suspension of the upper jaw (by means of the front pier of the arch structure), and moreover the zygomatic arch serves for the attachment of the chewing-muscles. If, all this notwithstanding, we discuss the suspension of the jaw joint apart from that of the upper jaw, and apart from the attachment of the chewing-muscles we make mistakes, because we separate things that cannot be separated, which will lead us into difficulties.

b. The size of the suspensorial mechanism of the jaw joint

As the suspensorial mechanism of the jaw joint consists of different elements in different groups, it would be logical to discuss the size of the suspensorial mechanism as a whole as well as the size of each of the constituent components. Here, too, we must discuss the absolute size besides the relative size.

The absolute size of the suspensorial mechanism of the jaw joint

Exact data on the absolute size of the suspensorial mechanism as a whole as well as on that of its component parts are not to be found in the literature I consulted.

So we shall have to content ourselves with the general remark that in large animal species this suspensorial mechanism generally will be large and in small ones it will be small. For the size of the suspensorial mechanism will be connected with the pressure exercised on the jaw joint and this shows a certain parallel with the size of the animal. Anyway in animal species with identical food which is seized, mastered and consumed in the same way. This parallel with the size of the animal is interfered with by other dependencies. Thus the size of the suspensorial mechanism of the jaw joint also depends on the use of the teeth in seizing, gripping and chopping up the food or the prey, and consequently it depends on the character of the food.

The relative size of the suspensorial mechanism of the jaw joint

On this subject no exact data can be found in literature either; neither on the suspensorial mechanism as a whole, nor concerning its component parts.

In stages of development

In the embryonic and larval stages of most Teleostei, the suspensorium is relatively long, because it is curved forward beneath the eye (GREGORY, 1933, pp. 422, 428).

In adult animals

As has been indicated already in the introduction we shall discuss these conditions for four classes of cases separately, *viz.* in Elasmobranchii, in the higher Pisces, in Amphibia and Sauropsida, and in Mammalia. In Elasmobranchii the jaw joint is situated on the pars quadrata of the palatoquadratum, which bears at the same time the dental plate and the place of origin of the chewing-muscles. In the higher Pisces we find a separate quadratum and the suspensorium is characterized by the strong development of the hyomandibulare. In Amphibia and Sauropsida the latter is not the case, but the joint is still between quadratum and articulare. Finally, in Mammalia we find a squamosum-dentale joint, so an entirely different suspensorial mechanism of the jaw joint.

In Elasmobranchii

Among Elasmobranchii the processus oticus of the quadratum, if present, is also relatively small.

We find considerable differences in the size of the hyomandibulare, dependent on the fact whether the suspension of the palatoquadratum is amphistylic (Notidanidae), autostylic (Holocephali) or hyostylic (most Elasmobranchii).

The size and development of the socket for the hyomandibulare on the sides of the neurocranium depends on the function of the hyomandibulare in the suspension of the pars quadrata of the palatoquadratum (HOLMGREN & STENSIÖ, 1936, p. 320). The neurocranium itself has been little changed in connection with the suspension of the jaw joint (MARINELLI, 1936, pp. 230/231).

In higher Pisces

We owe many data on the size of the suspensorial mechanism of the jaw joint in higher Pisces to **Gregory** (1933).

The measurements of the suspensorial mechanism in the different directions will be discussed separately.

The length of the elements of the suspensorial mechanism is seldom mentioned. In *Polyodon* the hyomandibulare is long (**Gregory**, 1933, p. 117, fig. 17).

The length of the suspensorium (see my fig. 143) is indicated by the length of the suspensorial line, which joins the suspensorial point (this point lies midway between the centres of the anterior and posterior facets for the hyomandibulare) with the quadratum pivot (that is the mid point of the articular hinge of the quadratum) according to **Gregory** (1933, p. 420). Taking into account what will, in the discussion of the situation, be called the suspensorial angle (the inclination of the suspensorial line to the horizontal) the length of the suspensorium may also be determined from the level of the quadratum-articulare centre, which we have come to know before, and the height of the hyomandibular socket, that is the height of its mid point above the horizontal; wherein this mid point is the point midway between the centres of the anterior and posterior facets for the hyomandibulare and wherein the horizontal is the line joining the prosthion and the pygidion, wherein the prosthion is the most anterior point of the snout and the pygidion the mid point of the narrowest part of the caudal peduncle (**Gregory**, 1933, p. 420). The socket for the hyomandibulare is always tripartite: sphenotic facet, proötic facet and pterotic facet (**Gregory**, 1933, p. 437). However, **Gregory** nowhere gives numbers concerning the length of this suspensorial line; he only gives a number of sketches, wherein this line is indicated (figs 286–290).

The length of the axis of the suspensorium is, however, determined by a line, generally curved, which is determined by the two ends of the suspensorial line; this curve originates when the suspensorium bends forward below the orbita, which is logical when the quadratum-articulare joint lies below or rostral of the orbita. So the length of the (curved) axis of the suspensorium is determined by the position of the top of the hyomandibulare with regard to the orbita, especially in a rostrocaudal direction, but also in a dorsoventral direction, and, secondly by the position of the quadratum-articulare joint with regard to the orbita in a rostrocaudal as well as in a dorsoventral direction. In general we may say that the axis of the suspensorium is relatively very short when the hyomandibulare is suspended immediately caudal of the orbita and the quadratum-articulare joint lies immediately behind the back edge of the orbita, and far dorsally.

A more rostral position of the quadratum-articulare joint, below the orbita and especially in front of the front edge of the orbita will increase the length of the axis of the suspensorium, because the suspensorium extends ventrally under the orbita. An extreme caudal position of the quadratum-articulare joint, far caudal of the back edge of the orbita will relatively increase the length of the axis of the suspensorium. A more ventral position of the quadratum-articulare joint will also relatively lengthen the axis of the suspensorium. Many examples of these situations, the more rostral one, the far caudal one and the more ventral one, we found in the paragraph concerned.

The relative length of the axis of the suspensorium is, however, also influenced by the position of the place of suspension of the hyomandibulare to the neurocranium, so of the top of the hyomandibulare. According to GREGORY (1933, p. 437) the support for the hyomandibulare is very appropriately located between the powerful postocular arch and the occipital buttress afforded by the lateral wing of the pteroticum. In very many cases the top of the hyomandibulare lies closely behind the back edge of the orbita. In the pictures where GREGORY indicates the position of the suspensorial point, this point lies in 20 out of 21 cases very close to the back edge of the orbita (figs 165, 286-290). *Lepisosteus* is clearly an exception to this (fig. 287 D; see also fig. 25 A). In the numerous pictures of skulls of Pisces given by GREGORY (1933) the position of the top of the hyomandibulare may be ascertained in a relatively large number of cases. In a large majority of these cases the top of the hyomandibulare lies at a very short distance from, sometimes immediately behind the back edge of the orbita. In some few cases the front edge of the most dorsal part of the hyomandibulare lies slightly caudal of the back edge of the orbita, but in these cases the upper edge of the hyomandibulare is so long that the top of the axis of the hyomandibulare lies nevertheless relatively far caudal of the back edge of the orbita. This is pictured for *Ophicephalus* (fig. 145 A), *Rhachycentron* (fig. 186) (see my fig. 120), *Cottus octodecimspinosus* (Mitchill) (fig. 212), *Lota* (fig. 258 B) and *Opsanus tau* (L.) (fig.

263 A). In a number of other cases the top of the hyomandibulare lies distinctly farther backward with regard to the back edge of the orbita. Among those cases the top of the hyomandibulare is, in *Lycodontis funebris* (Ranzani), so broad that the top of the axis of the hyomandibulare lies relatively far caudal of the back edge of the orbita (fig. 82 B) (see my fig. 119). Relatively far caudal of the back edge of the orbita lies the dorsally not extremely broadened hyomandibulare in *Amia calva* L. (fig. 28), *Esox masquinongy* Mitchill (fig. 95 A) (see my fig. 30), *Lates niloticus* (Gmel.) (figs 114, 298) (see my fig. 115), *Hippoglossus* (fig. 224) and *Anarhichas* (fig. 255). Extremely far caudal with regard to the back edge of the orbita lies the top of the hyomandibulare in *Notopterus* (fig. 61) and in *Symbranchus* (fig. 231) (see my fig. 123).

It is much more difficult to get a good insight in the position of the suspensorial point in a dorsoventral direction. We find varying conditions with regard to the lateral projection of the dorsal median as well as with regard to the orbita. In the pictures where Gregory indicates the position of the suspensorial point we find in 10 out of the 21 genera pictured, that the suspensorial point lies behind the orbita; in 10 it lies above the orbita (a.o. in all figured fossil † Palaeoniscidae and the Holostei) and in 1 (*Balistes*) it is situated ventral of the orbita (Gregory, 1933, figs 165, 286-290) (see my fig. 43). In the other pictures the position of the suspensorial point cannot be indicated exactly so that we shall refrain from classifying the conditions found in the numerous pictures. We shall only mention one or two striking examples. In *Periophthalmus* the hyomandibulare lies very low with regard to the orbita (fig. 228) (see my fig. 41). The upper edge of the hyomandibulare lies very high in *Diodon hystrix* L. (fig. 170) (see my fig. 121), *Clinus despicillatus* C.V. (fig. 251) and *Opsanus tau* (L.) (fig. 263 A).

We shall now discuss the relative length of the suspensorium in a general way, with regard to the four dependencies mentioned: the position of the quadratum-articulare joint in a rostrocaudal and in a dorsoventral direction, and the position of the suspensorial point in a rostrocaudal direction, and if possible also in a dorsoventral one. In doing so we shall start from the position of the quadratum-articulare joint in a rostrocaudal direction with regard to the orbita, because this position is in several respects so very important for the architecture of the skull. We shall first treat the genera in which Gregory (1933, figs 165, 286-290) indicates the exact position of the suspensorial point and of the quadratum-articulare joint and then a small selection of other examples without any claim to completeness. Therefore we shall not treat all the examples earlier mentioned in the discussion of the position of the quadratum-articulare joint. From this more data might be derived as might also from the following discussion of the position of the suspensorium.

When the quadratum-articulare joint is situated below and the suspensorial point lies immediately behind the back edge of the orbita, the suspensorial line will run vertically and therefore be relatively short. In the illustration where suspensorial point and quadratum pivot are pictured, *viz.* for *Platysomus* (fig. 286 D, see also fig. 15 B) (see my figs 90, 143 *b*), the suspensorial line has been relatively lengthened because the suspensorial point lies dorsal of the horizontal through the upper edge of the orbita and the quadratum pivot lies relatively far ventral of the horizontal through the lower edge of the orbita. From other pictures in Gregory we may point out the following cases. In † *Hoplopteryx lewesiensis* (Mantell) the suspensorial point lies also immediately behind the back edge of the orbita, so that the suspensorium is said to be nearly vertical, further it is said to be quite long, which stands to reason because the quadratum-articulare joint lies very far ventral and the suspensorial point lies on a level with the upper edge of the orbita (p. 233, fig. 110). In *Polynemus* (= *Polydactylus*) the quadratum-articulare joint lies almost directly beneath the mid point of the hyomandibulare, but as the quadratum-articulare joint shows a downward displacement, the suspensorium will be relatively long (p. 268). Judging from the picture of *Polydactylus* sp. (*Polynemus*), which is referred to (fig. 144), the upper edge of the hyomandibulare lies moreover on a level with the upper edge of the orbita. In *Esox masquinongy* Mitchill (fig. 95 A) (see my fig. 30), *Lates niloticus* (Gmel.) (figs 114, 298) (see my fig. 115), *Anarhichas* (fig. 255), *Lota* (fig. 258 B) and *Opsanus tau* (L.) (fig. 263 A) the suspensorial point lies comparatively far behind the back edge of the orbita, so that the axis of the suspensorium definitely slopes (in *Esox* only slightly slopes) from ventrorostral to dorsocaudal and is, consequently, relatively longer, which length is increased still, because the quadratum-articulare joint is situated far ventralward, whereas the suspensorial point lies far dorsal. The suspensorial point lies dorsal of the horizontal through the upper edge of the orbita in

Esox masquinongy Mitchill and in *Lates niloticus* (Gmel.), it lies on a level with the upper edge of the orbita in *Lota* and *Opsanus tau* (L.) and it lies on a level with the middle of the orbita in *Anarhichas*. In all these cases where the quadratum-articulare joint lies right under the back edge of the orbita, the axis of the suspensorium is straight or hardly curved at all, not more curved than the axis of the praeoperculum, which stands to reason because the suspensorium does not curve round the orbita.

In a second class of cases the quadratum-articulare joint definitely lies more or less far behind the back edge of the orbita. In the cases where the suspensorial point lies at a short distance behind the back edge of the orbita, the axis of the suspensorium will consequently slope from ventrocaudal to dorsorostral and be relatively longer. We find this in † *Cheirolepis*, where the suspensorium is said to be large and where we might have to deal with a primitive condition (pp. 85, 421, fig. 286 A, see also figs 12 A and 283 A) (see my figs 95, 143 *a*), † *Coccocephalus* (fig. 286 B, see also figs 12 C and 283 B) and † *Perleidus* (fig. 286 C, see also fig. 283 C). To this we may probably add † *Palaeoniscus macropomus* Agassiz (fig. 12 B). The length of the suspensorial line is increased still, because the suspensorial point is situated dorsal of the horizontal through the upper edge of the orbita and because in † *Coccocephalus* and in † *Perleidus* the quadratum pivot lies a little more ventralward than in † *Cheirolepis* where it is situated only slightly below the lower edge of the orbita. We may also add some examples derived from GREGORY's pictures, where, however, the suspensorial point and the quadratum pivot have not been indicated. According to GREGORY, however, (1933, p. 422) a far caudal situation of the quadratum-articulare joint is an exception among Teleostei. Among the examples GREGORY (1933, p. 422) gives in this connection the suspensorial point lies closely behind the back edge of the orbita in *Engraulis encrasicholus* (L.) (p. 147, fig. 40) (see my fig. 76), *Gonostoma elongatum* Gthr (fig. 53) and in *Stomias boa* (Risso) (fig. 56) where it may even be partly situated higher than the upper edge of the orbita. Because of this the suspensorium slopes in all these cases from ventrocaudal to dorsorostral, and is consequently relatively lengthened. In *Lycodontis funebris* (Ranzani) (p. 203, fig. 82 B) (see my fig. 119), however, which is also mentioned as an example by GREGORY (p. 422) in this connection, the suspensorial point lies comparatively far caudal behind the orbita, but not so far as the quadratum-articulare joint, so that here, too, the suspensorium slopes from ventrocaudal to dorsorostral, but less strongly so and consequently the suspensorial line will be shorter. This length of the suspensorium is, in the examples mentioned, increased because the quadratum pivot lies very far ventral (*Lycodontis*, *Gonostoma*) and because the suspensorial point lies, in all four cases, far dorsal *viz.* on a level with the upper half of the orbita (*Engraulis*), on a level with the upper edge of the orbita (*Lycodontis*), or even dorsal of the horizontal through the upper edge of the orbita (*Gonostoma*, *Stomias*). GREGORY (1933, p. 422) mentions these examples to illustrate the exceptional condition among Teleostei, of a far caudal position of the quadratum-articulare joint, adding that this also occurs in their allies and some others. To these belongs a.o. *Gastrostomus* (p. 416, fig. 94) (see my fig. 87), where hyomandibulare and quadratum are extremely long in connection with the far ventral and caudal position of the quadratum-articulare joint. Among the other figures in GREGORY (1933) I want to point out the following five cases. In *Synodus foetens* (L.) (p. 207, fig. 86) and *Saurus myops* (Bl. Schn.) (fig. 87 A) the suspensorial point lies at a short distance behind the back edge of the orbita, so that the suspensorium slopes from ventrocaudal to dorsorostral, and is consequently relatively lengthened; this slope is not very pronounced in *Saurus*, which may be connected with the fact that the quadratum pivot lies very far ventral, in contrast to *Synodus*. In consequence of this last mentioned extension the suspensorial line in *Saurus* is relatively long, relatively longer than in *Synodus*. In *Synodus*, however, the suspensorial point lies dorsal of the horizontal through the upper edge of the orbita, in *Saurus* it lies on a level with this upper edge. In *Ophicephalus* (pp. 269/270, fig. 145 A), *Notopterus* (fig. 61) and *Symbranchus marmoratus* Bl. (fig. 231) (see my fig. 123), however, the suspensorial point lies in the first case rather far, and in the two latter cases very far caudal of the back edge of the orbita, *viz.* farther caudal than the quadratum-articulare joint and consequently the suspensorium slopes from ventrorostral to dorsocaudal, most pronouncedly so in *Notopterus* where the suspensorial point lies very much farther caudal than the quadratum pivot. The less steep this slope, the longer the suspensorial line will, proportionally, be. There is yet another reason why the suspensorial line is in these three cases relatively long: the suspensorial point lies, in *Ophicephalus*, on a level with the upper edge of the orbita, and in the two other genera even dorsal of the horizontal through the upper edge of the orbita, in *Notopterus* even far dorsal of it. Moreover the quadratum-articulare joint is situated, in all three cases, rather far ventral, which also relatively lengthens the suspensorial line. In all these cases of the second class there is no question of the axis of the suspensorium being longer than the distance between the suspensorial point and the quadratum pivot, because the suspensorium would have to curve round the orbita. The curved shape of the suspensorium of *Gonostoma* (fig. 53) has a different cause, but nevertheless the axis is lengthened by it. We shall limit ourselves to these examples; doubtless there are more among the examples of the earlier mentioned third main type of the proportion between the length of the jaws to the length of the snout, in which main type the upper jaws are long and the snout is short.

In a third class of cases we shall include those examples where the quadratum-articulare joint lies below the orbita. In order to keep the same classification of examples followed before in the discussion of the position of the quadratum-articulare joint, we shall here, too, arrange the examples according to the fact whether the quadratum-articulare joint lies below the back edge or below the back half, below the centre, below the front half or below the front edge of the orbita.

As regards the position of the quadratum-articulare joint below the back edge or below the back half of the orbita, we find a picture of this condition with the position of the suspensorial point and the quadratum pivot indicated, in † *Acentrophorus*, † *Portheus*, *Chirocentrus* and *Tylosurus* (figs 287 A, 288 B, C, 289 A) (see my fig. 94). In all these four cases the suspensorial point lies immediately behind the back edge of the orbita, so that the length of the suspensorial line is relatively short. It is, however, relatively lengthened because the suspensorial point lies in *Chirocentrus* on a level with the upper edge of the orbita, in the other three cases even dorsal of the horizontal through this upper edge. In † *Portheus* (see also p. 144, fig. 36) and *Chirocentrus* as opposed to the other two genera, we find, moreover, that the quadratum-articulare joint lies far ventralward, which relatively increases the length of the suspensorial line. This condition occurs in the primitive protospondyl † *Acentrophorus* (pp. 85, 125, 421, fig. 287 A, see also fig. 21 B). In the primitive Teleostei the quadratum-articulare joint lies at about the same place as in † *Acen-*

trophorus (GREGORY, 1933, p. 421). In many later Teleostei also we find in the adult specimens that the quadratum-articulare joint lies ventral of the orbita because the forward curving of the suspensorium beneath the eye found in earlier developmental stages in many forms may tend to be retained in the adult (GREGORY, 1933, pp. 422/423, 431). By this forward inclination of the suspensorium its length is relatively increased. This increase of the length of the suspensorium is found among those cases where the quadratum-articulare joint lies ventral of the back edge or of the back half of the orbita, even in a species with secondary elongated jaws, as *e.g.* in *Tylosurus* (pp. 221, 421/422, fig. 289 A, see also fig. 99) (see my fig. 94). From the series of pictures given by GREGORY where the exact position of the suspensorial point and of the quadratum pivot has not been indicated, we select the following three cases: *Tarpon atlanticus* (C. & V.) (p. 138, fig. 31) (see my fig. 85), *Cottus octodecimspinosus* (Mitchill) (fig. 212) and *Clinus* (fig. 251). In all three the quadratum-articulare joint lies far ventralward so that the length of the suspensorial line is relatively increased. Moreover in *Cottus* the suspensorial point is situated relatively far caudal of the back edge of the orbita, whereas this point is situated at a short distance behind the orbita in the two other genera. In *Tarpon*, however, the suspensorial point lies dorsal of the horizontal through the upper edge of the orbita and in *Clinus* it lies on a level with this upper edge, whereas in *Cottus* the suspensorial point lies on a level with the upper half of the orbita.

In † *Semionotus* (pp. 125, 125/127, fig. 287 B) and in † *Leptolepis* (fig. 288 A) the quadratum-articulare joint is situated right under the centre of the orbita. In both cases the suspensorial point lies at a short distance behind the back edge of the orbita. The length of the suspensorial line is, however, relatively increased because in both cases the quadratum pivot lies far ventralward, while the suspensorial point is situated, in † *Leptolepis* on a level with the upper edge of the orbita, and in † *Semionotus* even dorsal of the horizontal through the upper edge of the orbita. From the pictures given by GREGORY where the exact position of the suspensorial point and the quadratum pivot has not been indicated, we add the following three examples: *Lachnolaimus maximus* (Walbaum) (p. 257, fig. 130) (see my fig. 129), *Diodon hystrix* L. (fig. 170) (see my fig. 121) and *Rhachycentron* (fig. 186) (see my fig. 120). In *Rhachycentron* the length of the suspensorial line is relatively increased because the suspensorial point lies relatively far caudalward and at the same time dorsal of the horizontal through the upper edge of the orbita, but on the other hand the quadratum pivot does not lie very far ventralward. The latter does occur in *Diodon* and especially in *Lachnolaimus* where the suspensorial point lies indeed at a short distance behind the orbita, but in *Diodon* the suspensorial point is situated on a level with the upper edge of the orbita, and in *Lachnolaimus* it lies on a level with the upper half of the orbita. All this implies that the suspensorium is long or very long in all three cases. A further increase of the length of the suspensorium may be imagined, owing to the fact that the suspensorium must curve forward, round the orbita. The direction of the straight connecting line between the suspensorial point and the quadratum pivot in † *Semionotus* and † *Leptolepis* (figs 287 B, 288 A) shows that the axis of the suspensorium must be more curved. Probably, however, this curve is not stronger than that which is found in conjunction with a more caudal position of the quadratum-articulare joint, and which agrees with the rather commonly occurring faint curve of the axis of the praeoperculum (such as *e.g.* in *Clinus*, fig. 251). Such a faint curve is met with in *Rhachycentron* and in *Diodon*. In *Lachnolaimus maximus* (Walbaum), however, the axis of the suspensorium is practically straight, notwithstanding the position of the quadratum-articulare joint below the centre of the orbita. This is undoubtedly due to the very far ventralward position of the quadratum-articulare joint.

Below the front half or below the front edge of the orbita lies the quadratum-articulare joint in † *Lepidotus* (pp. 125, 125/127, fig. 287 C, see also fig. 22 B) and in † *Antennarius* (pp. 391, 392, 393, fig. 288 D, see also figs 265, 266), where the exact position of the suspensorial point and the quadratum pivot has been indicated. In both genera the suspensorial point lies at a short distance behind the orbita, but for the rest the position of the points determining in general the length of the suspensorial line, is rather divergent. In † *Lepidotus* the suspensorial point lies dorsal of the horizontal through the upper edge of the orbita; in † *Antennarius* it lies on a level with the centre of the orbita; in † *Lepidotus* the quadratum-articulare joint lies rather high, in † *Antennarius* it lies far ventralward. From the pictures given by Gregory we may add the following examples, where, however, the exact position of the suspensorial point and the quadratum pivot has not been indicated: *Albula vulpes* (L.) (p. 144, fig. 37) (see my fig. 125), *Dorosoma erebi* (Gthr) (*Chatoëssus erebi*) (p. 147, fig. 39) (see my fig. 29), *Priacanthus* (p. 247, fig. 120), *Hoplegnathus* (p. 250, fig. 124), *Capros aper* (L.) (p. 273, fig. 149 A), *Chaetodon ocellatus* Bl. (p. 279, fig. 155) and *Periophthalmus* (fig. 288, see however p. 347) (see my fig. 41). Only in *Periophthalmus* does the suspensorial point lie at some distance behind the orbita, which, in principle, entails a lengthening of the suspensorial line, in all other cases the suspensorial point lies immediately behind the orbita. This relative lengthening in *Periophthalmus* is, however, abolished because the suspensorial point lies below the horizontal through the lower edge of the orbita. In all other cases the suspensorial point lies a little above the centre of the orbita (*Priacanthus*) or on a level with the upper half of the orbita (*Capros aper* (L.)) or on a level with the upper edge of the orbita. A comparative lengthening of the suspensorial line is found in *Priacanthus*, *Hoplegnathus*, *Capros*, *Chaetodon* and *Periophthalmus*, where the quadratum pivot lies far, sometimes very far ventralward, in contrast with its position in *Albula* and *Dorosoma* (*Chaetoëssus*) where it is more dorsal with regard to the horizontal through the lower edge of the orbita. As in all these cases the quadratum-articulare joint has an advanced forward position *viz.* below the front half of the orbita or below the front edge of the orbita, we may in principle expect the axis of the suspensorium to be lengthened, because the suspensorium must curve forward beneath the orbita. We see that this is indeed the case in † *Lepidotus* (fig. 287 C) where both suspensorial point and quadratum pivot are situated high. The position of both points is also high in *Albula* and *Dorosoma* (*Chaetoëssus*) where, consequently, the axis of the suspensorium is bent, which increases the relative length of it. In † *Antennarius*, however, the axis of the suspensorium is not bent, owing to the fact that the suspensorial point as well as the quadratum pivot are situated low with regard to the horizontal through the lower edge of the orbita. In the other cases treated, however, the axis of the suspensorium is straight, anyway not definitely bent, owing to the far ventralward position of the quadratum-articulare joint, by which the suspensorium does not curve below the orbita. Only in *Chaetodon* the axis of the suspensorium is curved, notwithstanding the far ventralward position of the quadratum-articulare joint, but here the suspensorial point is situated not only far dorsalward, but also extremely close behind the back edge of the orbita. Here the line of the suspensorium has been relatively lengthened in connection with the curve in the axis of the suspensorium.

In a fourth and last class of cases we include those examples where the quadratum-articulare joint lies rostral of the vertical through the front edge of the orbita. This may be comparatively close in front, but it may also be exceptionally far in front of it.

At a short distance in front of the vertical through the front edge of the orbita lies the quadratum-articulare joint in *Lepisosteus* (p. 421, fig. 287 D, see also fig. 25 A; HOLMGREN & STENSIÖ, 1936, fig. 363) (see my fig. 65), where GREGORY indicates the exact position of the suspensorial point and of the quadratum pivot. So here we meet with a far rostral position of the quadratum-articulare joint, notwithstanding the fact that the jaws are secondarily elongated. In *Lepisosteus* the length of the suspensorial line is relatively increased, because the suspensorial point lies very far behind the back edge of the orbita, and a good way dorsal of the horizontal through the upper edge of the orbita. A relative lengthening of the suspensorial line due to the position of the quadratum pivot does not occur, because this point lies very high. It is probably also due to this fact that, notwithstanding the far caudal position of the suspensorial point, the axis of the suspensorium is curved, so that the length is relatively increased. To this we may add the following examples from the illustrations in GREGORY, wherein, however, neither the exact position of the suspensorial point nor that of the quadratum pivot have been indicated: *Sternoptix* (p. 158, fig. 52 B), *Gymnarchus niloticus* Cuv. (p. 173, fig. 62 B) (see my fig. 82), *Microspathodon chrysurus* (C.V.) (p. 255, fig. 128), and *Zeus japonicus* C. V. (p. 272, fig. 148). In all these four cases the suspensorial point lies immediately behind or near the back edge of the orbita, so that the length of the suspensorial line is not relatively lengthened. In *Gymnarchus* the quadratum-articulare joint lies rather far dorsal, while at the same time the suspensorial point lies on a level with the horizontal through the lower edge of the orbita. By these two circumstances the suspensorium is not only relatively very short, but its axis is, at the same time, straight. In the other three cases the quadratum-articulare joint lies far ventral and the suspensorial point lies on a level with the upper edge of the orbita (in *Microspathodon* only it lies on a level with the centre of the orbita). Consequently, the axis of the suspensorium is, in these three examples, curved, by which the length of the suspensorium is relatively increased; in *Microspathodon* this is the case notwithstanding the fact that the suspensorial point lies on a level with the centre of the orbita, but the quadratum pivot lies rather far in front of the vertical through the front edge of the orbita.

In a number of allied genera from a few separate groups the quadratum-articulare joint lies very far rostral with regard to the vertical through the front edge of the orbita. GREGORY (1933) indicates the exact position of the suspensorial point and the quadratum pivot in the following cases. They have been arranged according to the increasing distance between the quadratum-articulare joint and the vertical through the front edge of the orbita: *Pomacanthus* (fig. 290 A, see also fig. 154), *Teuthis* (fig. 165, see also fig. 159), *Triacanthus* (fig. 165, see also fig. 160), *Xesurus* (fig. 290 B, see also fig. 157), *Balistes* (fig. 165, see also fig. 161) (see my fig. 43), *Alutera* (figs 165, 290 C, see also fig. 163) (see my fig. 91), *Anacanthus* (fig. 165) and *Fistularia* (fig. 289 B, pp. 225, 418, see also fig. 105) (see my fig. 93). In this order the relative distance between the quadratum-articulare joint and the vertical through the front edge of the orbita, and consequently the relative length of the suspensorium, increase. In all these cases the suspensorial point lies at a short distance behind the back edge of the orbita, but there are some differences in the height at which this point lies. Thus, in *Teuthis*, the suspensorial point lies on a level with the upper edge of the orbita, in *Pomacanthus*, *Triacanthus*, *Xesurus*, *Anacanthus* and *Fistularia* it lies on a level with the centre of the orbita, in *Alutera* it lies on a level with the lower edge of the orbita, while in *Balistes* the suspensorial point is situated ventral of the horizontal through the lower edge of the orbita. All this, however, has no great importance for the relative length of the suspensorial line. In principle the position of the quadratum pivot in a vertical direction is more important in this respect: in *Fistularia* this point lies rather high, in all the other genera mentioned it lies, however, far ventral so that the length of the suspensorial line is relatively increased. In the genera mentioned we may expect the axis of the suspensorium to be curved, because it must curve below the orbita so that a relative lengthening of the suspensorium is brought about. In *Balistes* and *Alutera*, however, the suspensorial point lies so low that the suspensorium need not be curved below the orbita (the slight curve in the suspensorium of *Balistes* runs parallel with that of the praeoperculum). In *Pomacanthus* it is not necessary either for the suspensorium to curve below the orbita, owing to the exceptionally far ventral position of the quadratum-articulare joint combined with a not so very far rostral position. Examples of similar cases with an extreme prolongation of the suspensorium may also be found in other genera from the groups of the Chaetodontoidei, "Teuthidoidei", Zanclidae, and Balistidae (pp. 282, 284, 422, 438, figs 154-165) (see my figs 43, 91, 117) and from the Thoracostei (figs 102-109) (see my figs 93, 143 *d*). At the same time they are representatives of the first main type of the proportion between the length of the jaw and that of the snout, in which main type the snout is long and the upper jaw short.

The breadth of the suspensorium is, in general, considerable along its entire length. It is true that the symplecticum is generally narrow, but in that case the adjacent metapterygoid is usually broad (see however *Mistichthys luzonensis* H. M. Smith, in GREGORY, 1933, fig. 230).

A broad suspensorium is connected with a strongly developed upper jaw. As GREGORY (1933, p. 438, fig. 82 B) (see my fig. 119) mentions, in large-mouthed predaceous fishes, such as Apodes, the hyomandibulare is huge; in the picture to which he refers, *viz.* that of *Lycodontis funebris* (Ranzani) the broad hyomandibulare is joined immediately to the quadratum. Furthermore GREGORY mentions of *Gasteropelecus* (1933, p. 185) that the suspensorium is broad. In a number of Thoracostei (figs 104-108) with a very long snout, at the end of which is situated a short upper jaw, the condition is peculiar, because a narrow hyomandibulare is joined to a very broad metapterygoid and quadratum, which is connected with the development of the protruding snout.

A very narrow suspensorium is found in *Gastrostomus* where, according to GREGORY (1933, pp. 212, 416, fig. 94) (see my fig. 87) the hyomandibularia are slender hoops and the quadrata are rod-like. In a number of other cases, too, a narrow suspensorium is pictured where only the two ends of the hyomandibulare or quadratum are a little broader; such a narrow suspensorium is connected with a weakly developed jaw. We find this a.o. illustrated in GREGORY (1933) for: *Argyropelecus* (fig. 52 A), *Sternoptix* (fig. 52 B), *Gonostoma elongatum* Gthr (fig. 53), *Cyclothone microdon* (Gthr) (fig. 54), *Chauliodus sloanei* (Bl. Schn.) (fig. 55) (see my fig. 122), *Lestidium speciosum* Bellotti (fig. 88), *Stylophorus* *chordatus* Shaw (fig. 176), *Bregmaceros atlanticus* Goode & Bean (fig. 261), *Melanocetus niger* Regan (fig. 272 B), "*Cryptosparas*" (in my opinion *Cryptopsaras*) (fig. 273), *Lophodolos* (figs 274, 276 A) and *Oneirodes* (fig. 279).

This suspensorium is suspended to the skull. In the above we mentioned the facets to which it is attached. The degree of development of this place of suspension must be related to the development of the suspensorium itself. According to GREGORY (1933, p. 438, fig. 82 B) the point of attachment of the hyomandibulare to the neurocranium is strongly built in large-mouthed, predaceous fishes, as in Apodes.

In Amphibia and Sauropsida

In Amphibia and Sauropsida we find, as in the higher Pisces, that it is the quadratum which is suspended to the neurocranium, because the quadratum bears the jaw joint. Contrary to the condition in the higher Pisces, however, is the fact that the hyomandibulare has no part in the suspensorial mechanism of the jaw joint. Only in a single Reptile the so-called intercalare of VERSLUYS has been found between quadratum and processus paroticus, which intercalare is supposed to represent a rest of the hyomandibulare. However important this point may be for comparative anatomy, for the architecture of the skull this very small element is of little importance.

In general we may say that in these groups, too, the suspensorial mechanism of the jaw joint is well developed when the upper jaw is powerful, and weakly developed when the upper jaw is weak. This is, in its turn, connected with the pressure exercised in biting and chewing, so with the use of the teeth in seizing, holding and chopping up the food and consequently also with the character of the food. Thus the suspensorial mechanism of the jaw joint is strongly developed when the prey is big, and the dentition is strong or specialized; see *e.g.* Loricata. The suspensorial mechanism of the jaw joint is weakly developed with simple gripping-teeth and a very mobile, not powerfully struggling prey *etc.*, see *e.g.* Amphibia, Sauria. The same occurs in Aves.

The processus oticus, which occurs among Amphibia, is also relatively a small processus.

The quadratum itself is generally strongly developed, also in animals with a relatively weakly developed suspensorial mechanism of the jaw joint. According to MARINELLI (1929, pp. 133/134/135) (see my fig. 151) who has analyzed the very different conditions in *Hydrosaurus* (*Lophura*), *Sphenodon* (*Hatteria*) and *Iguana*, the lateral cylindrical condylus ("laterale Gelenkrolle") of the jaw joint finds in *Hydrosaurus* (*Lophura*) its buttress in the column of the body of the quadratum; in *Iguana* this part of the jaw joint is only partly buttressed by this column and for the greater part by a thickening of the front edge of the frame of the tympanic membrane; in *Sphenodon* the part in question finds its buttress in the part of the quadratum covered by the quadratojugale.

In a number of groups, such as in Sauria, Serpentes and Testudinides the quadratum is suspended to a processus paroticus which is also strongly developed when the upper jaw is not especially strongly developed in connection with a very mobile, not powerfully struggling prey, a primitive set of gripping-teeth *etc*. In † Stegocephala and in † Seymouriamorpha among the Reptilia the quadratum does not extend upwards so far that it can reach the processus paroticus (VERSLUYS, 1936, pp. 700/701, 703). In *Hydrosaurus* (*Lophura*) the column of the quadratum is, according to MARINELLI (1929), buttressed by the "processus paroccipitalis" (processus paroticus). In Amphibia, Loricata and Aves the processus paroticus is lacking and the quadratum is directly attached to the lateral wall of the neurocranium.

Apart from these chondrocranial connections we also find connections with covering bones of the secondary cranial roof. This is in nearly all cases brought about by means of the zygomatic arches, but in the stegocrotaphic skulls of † Cotylosauria and Testudinides the quadratum is also attached to adjacent bones of the secondary cranial roof.

The suspension of the quadratum and with it of the jaw joint, to the zygomatic arches, is treated by MARINELLI as the hanging part of a bridge-like structure beside the suspension of the quadratum as the backmost pier of this construction (MARINELLI, 1929, p. 132; 1933, p. 203). Apart from this the zygomatic arches have other functions but we have exhaustively discussed the general side of this question before, and shall here only make some directly applicable remarks. In any case, the zygomatic arches must be regarded in connection with the suspension of the jaw joint (VERSLUYS according to MARINELLI, 1933, pp. 202/203, 203/204). Among the Reptilia examined by Marinelli (1929, pp. 133/134/135) we find that, in *Hydrosaurus* (*Lophura*), the quadratum is not only buttressed by the processus paroticus, but also by the posttemporal arch, joined by the horizontal upper zygomatic arch (the lower one is lacking); in *Iguana* the upper zygomatic arch which slants upwards and rostralwards towards the cranial roof, constitutes the principal attachment of the quadratum to the cranial roof, so that the quadratum, and with it the jaw joint, is firmly attached to the outer cranial wall (a lower zygomatic arch is lacking in this case too); in *Sphenodon* finally, it is the lower zygomatic arch that intercepts the pressure of the joint undergone by the quadratum; this is connected with the fact that it is the part of the quadratum covered by the quadratojugale that buttresses the jaw joint.

As the pressure exercised on the jaw joint is transmitted farther on, we see that the part of the skull dorsal of the jaw joint, is generally firmly constructed (Marinelli, 1929, p. 133; 1933, p. 203).

In Mammalia

In Mammalia the jaw joint is a squamosum-dentale joint, so entirely different from that of Non-Mammalia; consequently its suspensorial mechanism is entirely different too. In Mammalia the important thing is the suspension of the squamosum.

In the firm attachment of the squamosum the important point is especially the development of the medial high part of the skull, with the temporal wall and the crista occipitalis, so that part of the skull which lies dorsal of the jaw joint and to which the pressure excercised on the joint is in the first place transmitted (Marinelli, 1929, p. 133; 1933, p. 203).

In *Giraffa camelopardalis* (L.) the medial part of the jaw joint, which, as a whole, has a far medial position, is most strongly developed and is entirely buttressed by the sidewall of the skull in the temporal region, under which it is situated; the zygomatic arch is not necessary for the buttressing of this medial part (Marinelli, 1933, pp. 210, 211). In Pecora the jaw joint, which generally has a far medial position, is sufficiently fixed against the pressure exercised on the joint by the crista occipitalis.

Also in the oldest fossil Equidae, which were small, so that consequently the squamosum was strong enough to bear the pressure exercised on the joint and where the fossa glenoidea had not yet been shifted rostralwards and lateralwards, as is the case in recent Equidae, the fossa glenoidea is very strongly attached to the crista occipitalis (MARINELLI, 1933, p. 218). In recent Equidae we find other conditions as we shall see.

The zygomatic arch too, plays a part in the suspension of the jaw joint. The pressure on the jaw joint, will be transmitted on the zygomatic arch as midle part of the bridge-like construction. In the Mammalia mentioned above the zygomatic arch only played a subordinate part in the suspension of the jaw joint. In other cases, that will be discussed now, the zygomatic arch plays the chief part in the attachment of the jaw joint to the skull, according to MARINELLI.

In Carnivora, and to an extreme degree so in Felidae, the caudal downward slanting part of the zygomatic arch buttresses the fossa glenoidea against the pressure exercised on the joint; the rostral part of the zygomatic arch is bent upward, correlated with a very powerful musculus masseter (MARINELLI, 1929, p. 138; 1933, pp. 204, 209, 210) (see my figs 6, 7, 8, 48).

In Ungulata the zygomatic arch has been relieved by the displacement of the origin of the musculus masseter, consequently it has become weaker and has stretched and is no longer fit to be an independent buttress ("Widerlager") against the pressure exercised on the joint, nor, for the matter of that, against the chewing-pressure (MARINELLI, 1933, pp. 204/205). MARINELLI (1933, pp. 209, 210, 211) works this out in detail for *Giraffa camelopardalis* (L.): the origin of the musculus masseter lies here lower than the jaw joint, so that this muscle cannot exercise pressure, but at most pull on the jaw joint, against which the relatively weak processus zygomaticus squamosi offers sufficient resistance; the musculus pterygoideus can hardly exercise a pressure on the joint worth mentioning either; only the musculus temporalis has a slightly more favourable position.

In *Equus caballus* L. the zygomatic arch has a relatively massive structure, which, doubtless, is connected with the fact that the pressure on the joint exercised by the musculus masseter reaches the zygomatic arch at a very steep angle ("in einem sehr steilen Winkel"; very probably is meant at nearly right angles); the medial and the middle part of the jaw joint is sufficiently buttressed by the zygomatic arch against the pressure exercised on the joint by the musculus temporalis; in the attachment of the lateral part of the jaw joint the postorbital bar is material, as we shall see (Marinelli, 1933, pp. 212, 213) (see my fig. 149). For the postorbital bar may also play a part in the attachment of the jaw joint.

In *Giraffa camelopardalis* (L.) this is an additional function of the postorbital bar, *viz.* against the pressure on the joint exercised by the musculus temporalis; its main function in *Giraffa camelopardalis* (L.) is, however, the consolidation of the attachment of the back-teeth to the skull (Marinelli, 1933, p. 210) (see my fig. 150).

In *Equus caballus* L., however, the significance of the postorbital bar is entirely different: here its main function is the buttressing of the jaw joint (Marinelli, 1933, pp. 205, 213-219). Contrary to the medial and central parts, the lateral part of the jaw joint, which is extended very much laterally, does not find sufficient support in the zygomatic arch, whereas it needs indeed a very strong buttress against the powerful pressure on the joint exercised by the musculus masseter and musculus temporalis. The postorbital bar functions as such, and is at the top supported by the firm cranial roof. In *Equus caballus* L. the postorbital bar runs from the back upper edge of the orbita, slanting backward and downward towards the region of the jaw joint, more especially in the direction of the tuberculum articulare. The fact that the bar is formed by a very long processus postorbitalis *s.* zygomaticus of the frontale, which is met by a processus zygomaticus of the squamosum, coming from the region of the jaw joint, whereas the jugale does not take part in the structure of the postorbital bar, also points to the function of this bar. Finally the direction of the back edge of the postorbital bar points to its function as buttress for the jaw joint. In all these points the postorbital bar of *Equus caballus* L. differs from that of *Giraffa camelopardalis* (L.), where its function also is different as we saw in the discussion of the suspension of the upper jaw. In *Equus caballus* L. a very firm buttress of the lateral part of the socket of the jaw joint is necessary because the peculiar chewing-motion of *Equus caballus* L. alternately lifts right and left condylus from the fossa glenoidea, and shifts these condyles to the more laterally situated tubercula articularia, thus causing a greater pressure on these tubercula. After the condylus has slipped back in the fossa glenoidea, a strong pressure is exercised there, too. Marinelli points out that these conditions and this function of the postorbital bar have only developed in the course of the phylogeny of the Equidae, during which the postorbital bar also is only gradually completed.

c. The position of the suspensorial mechanism of the jaw joint

In treating the size of the suspensorial mechanism of the jaw joint topographical moments played a very important part. For many details this discussion may be referred to, and we can here limit ourselves to discussing the following data.

In stages of development

In embryonic and larval stages of most Teleostei the suspensorium is curved forward beneath the eye and is arranged around the eye as a centre (GREGORY, 1933, pp. 422/423, 428, 450).

In adult animals

We shall in this section keep to the same division according to groups as was followed in the discussion of the size of the suspensorium.

In Elasmobranchii

In the hyostylic Selachii the hyomandibulare is directed obliquely backward and downward (GREGORY, 1933, pp. 117/118, fig. 17). The head of the hyomandibulare lies against the otical region of the neurocranium.

In higher Pisces

In this connection we shall discuss the general slope of the suspensorium and after that its position with regard to the orbita and the praeoperculum, and finally the position of the top of the hyomandibulare and of the ventral end of the suspensorium.

As regards the general slope of the suspensorium, we shall begin by pointing out that, according to GREGORY (1933, pp. 117/118) in *Polyodon* the hyomandibulare is directed obliquely backward and downward and that according to HOLMGREN & STENSIÖ (1936, pp. 398/399, 415, 420, 426) the hyomandibulare in † Palaeoniscidae and † Belonorhynchidae (Saurichthyidae) shows a marked slope from dorsorostral to ventrocaudal, that this is to a lesser degree the case in Perleididae, and to an even lesser one in Ospiidae. We owe a very great number of data on the slope of the suspensorium to GREGORY (1933). In this connection GREGORY (1933, p. 420) speaks of the suspensorial angle *i.e.* the inclination of the suspensorial line to the horizontal. In this definition the suspensorial line is the line which joins the suspensorial point (this point lies midway between the centres of the anterior and posterior facets for the hyomandibulare) with the quadratum pivot (this is the mid point of the articular hinge of the quadratum). The horizontal is the line joining the prosthion and the pygidion, the prosthion being the most anterior point of the snout and the pygidion the mid point of the narrowest part of the caudal peduncle (Gregory, 1933, p. 420) (see my fig. 143). In treating the size of the suspensorium of the jaw joint we have treated a number of examples of different positions of this suspensorial line. We refer to these here, and shall only cite what Gregory himself mentions in his text.

The suspensorium is primitively inclined backward, says Gregory (1933, p. 421, see also p. 85), as in the primitive † Palaeoniscidae, such as † *Cheirolepis*. In the palaeoniscoid † Catopteridae we have evidence that a downwardly directed suspensorium has been derived from a backwardly inclined one (Gregory, 1933, p. 116).

The Teleostei appear to have been derived from forms as † *Acentrophorus* with a forwardly inclined suspensorium (Gregory, 1933, p. 421, see also p. 203). The forward curving of the suspensorium beneath the eye in the early developmental stages may in these forms tend to be retained in the adult (pp. 422/423). The suspensorium in adult Teleostei retains its forward inclination, even after the jaws become secondarily elongated, as in *Lepisosteus* and in *Tylosurus* (pp. 421/422). In the discussion of the † *Acentrophorus* mentioned, Gregory (1933, p. 125) states, however, that the suspensorium is vertical or inclined forward. Gregory (1933) mentions a great number of cases of a forward inclination of the suspensorium, *viz.* for the more recent † Semionotidae (p. 125), *Albula* (p. 144), *Dorosoma* (*Chatoëssus*) (p. 147), *Opisthoproctus* (p. 151), *Cromeria* (p. 155), *Gasteropelecus* (p. 185), *Anguilla chrysypa* Raf. (*Anguilla rostrata*) (p. 203), *Umbra krameri* Fitzinger (p. 216), *Fundulus* (pp. 217, 223), *Anableps tetrophthalmus* Bl. (p. 220), *Tylosurus* (pp. 221, 223), *Hemirhampus* (p. 223), *Halocypselus* (p. 223), *Fistularia* (p. 225), *Sphyraena* (pp. 266, 267), Esocidae (p. 267), Apodes (p. 267), Chaetodontoidei, "Teuthidoidei", Zanclidae and Balistidae (pp. 281/282, 282/283, 284, 422, 438), *Luvarus* (p. 306), Gobioidei (p. 346) and *Symbranchus* (p. 352). Here and there Gregory makes an observation on the degree of the forward inclination, from which I mention his pointing out that, among Balistoidei, a progressive forward swing of the suspensorial line occurs (p. 422) and that, with regard to the inordinately forward produced position of the suspensorium, nothing approaching the condition in *Fistularia* is known outside its own group (p. 225).

As an exception among Teleostei the suspensorium is backwardly inclined (GREGORY, 1933, p. 422). This is the case in *Engraulis encrasicholus* (L.) (pp. 147, 422), *Coila* (p. 147), *Lycodontis funebris* (Ranzani) (pp. 203, 422, 438), *Gonostoma elongatum* Gthr (p. 422), *Stomias boa* (Risso) (p. 422), *Gastrostomus* (p. 213), *Stylophorus chordatus* Shaw (p. 300) and the Apodes in general among the large-mouthed predaceous Pisces with a suspensorium showing an obliquely backward inclination (p. 438). Further GREGORY (1933, p. 207) mentions that *Synodus* and its allies are more specialized than *Aulopus* in the backward inclination of the suspensorium.

Among Teleostei GREGORY (1933, p. 233) mentions of † *Hoplopteryx lewesiensis* (Mantell) that the suspensorium is nearly vertical.

While we can practically always speak of the inclination and position of the suspensorium, as a certain, fixed phenomenon in a certain species, we see that, in some cases this is not so, because the quadratum is movable with regard to the hyomandibulare. In the most extreme stage of protrusility of the upper jaw, as *e.g.* in *Epibulus*, even the quadratum, which is fixed by the surrounding bones in all preceding stages has acquired a flexible joint with the hyomandibulare (GREGORY, 1933, pp. 257, 424).

As regards the position of the suspensorium with regard to the orbita, we refer to the discussion of the size of the suspensorium, in which the position with regard to the orbita played such an important part. We will only add the following observations from GREGORY. With reference to the forward migration and displacement of the quadratum-articulare joint, which implies a forward inclination of the suspensorium, he mentions that this would cause the circular pattern around the eye (p. 125), which points to a position close to the eye, and that the extreme condition of the forward inclination of the suspensorium in the "Teuthidoidei", Zanclidae and Balistidae has led to the very strange result that the hyomandibulare now comes into direct contact with the circumorbital bones, which become fastened to it (pp. 281/282).

The suspensorium lies rostral of the praeoperculum and is in general parallel to it. This clearly follows from the observation in Gregory (1933, p. 414) that lateral warping and vertical stretching of the hyomandibulare-symplecticum-quadratum series is prevented by the lunate praeoperculum, which is wrapped tightly around the back of the quadratum-symplecticum and hyomandibulare.

As regards the position of the dorsal end of the suspensorium, *viz.* the top of the hyomandibulare, the reader is referred to the discussion of the size of the suspensorium, where this very position of the top of the hyomandibulare with regard to the dorsal median of the skull, but especially with regard to the orbita, played such an important part.

As regards the position of the ventral end of the suspensorium, *viz.* the quadratum-articulare joint, the reader is referred to the discussion of this point in the paragraph on the jaw joint and that on the size of the suspensorium.

In Amphibia and Sauropsida

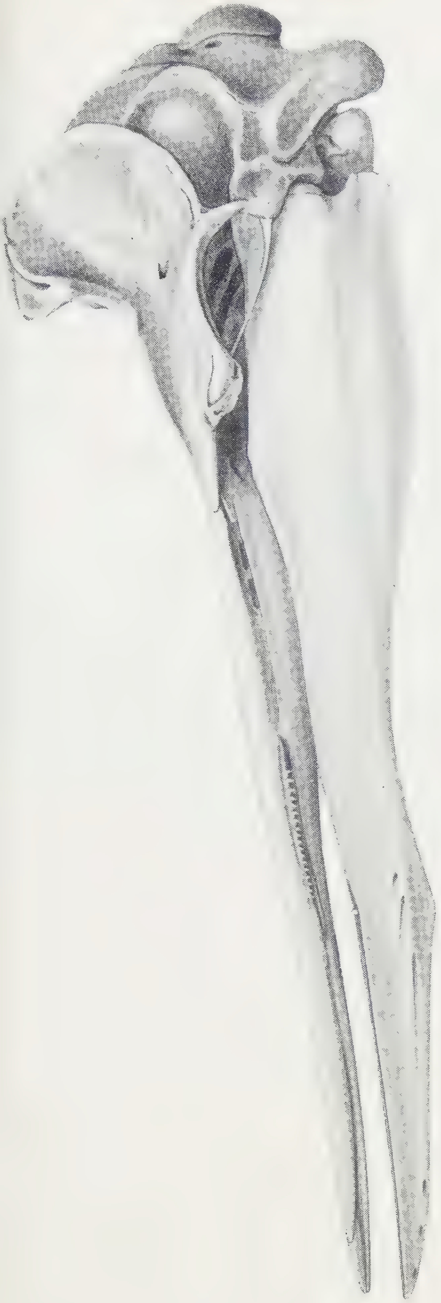
A discussion of the position of the quadratum, the zygomatic arches *etc.* seems superfluous. We shall limit ourselves to pointing out that the position in a certain species, is not always the same, when the skull shows kinesis, so that the quadratum is movable with regard to the processus paroticus. Kinesis may occur with a very mobile, not powerfully struggling prey, a simple, primitive gripping set of teeth, a weak structure of the upper jaw and of the suspensorium of the jaw joint. Akinesis, however, occurs with a powerfully struggling prey and strong, specialized teeth.

In Mammalia

A special discussion of the position of squamosum, zygomatic arch, postorbital bar *etc.* seems unnecessary.

d. Homology and non-homology

In general we cannot expect homology, because the conditions in different groups diverge too much. We shall only mention the suspensorium of the higher Pisces and the squamosum in Mammalia. There are also differences even within such a group. Thus the processus otici of the quadratum are, according to certain authors, not homologous with one another. Thus we find, among the higher Pisces, suspensoria with but also without a symplecticum (Gregory, 1933, pp. 155, 203), and the construction of the postorbital bar is not always identical.



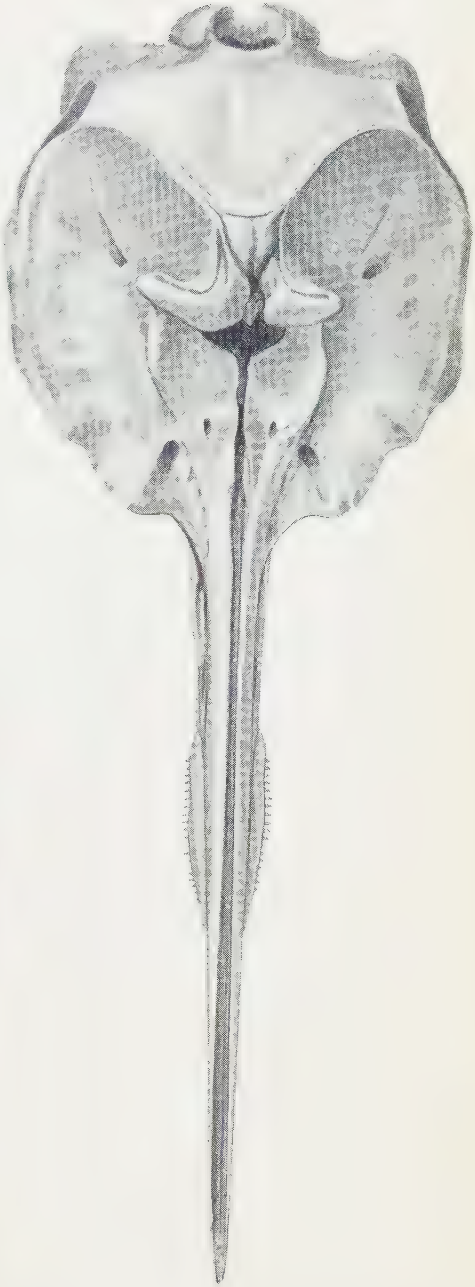


Fig. 70. *a. Mesoplodon grayi* von Haast ♀. Skull seen from the left side. R.M.N.H. Leiden, no. 1638. 0.2×. Original drawing by M. A. Koekkoek.

Fig. 70. *b. Mesoplodon grayi* von Haast ♀. Skull seen from above. R.M.N.H. Leiden, no. 1638. 0.2×. Original drawing by M. A. Koekkoek.

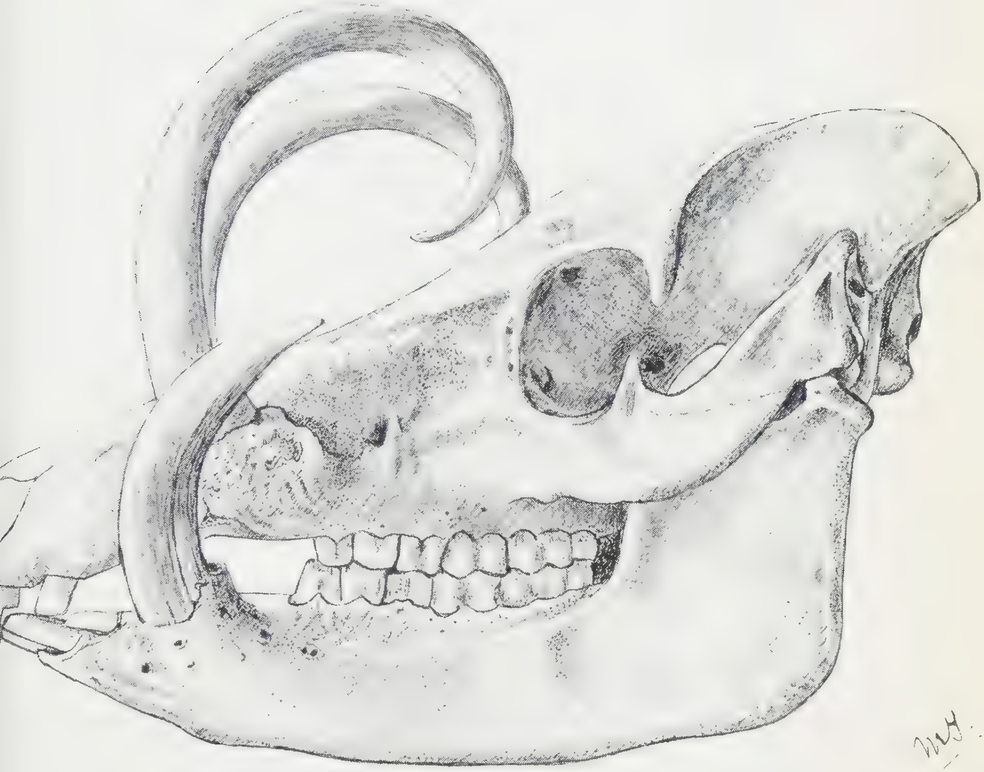


Fig. 71. *Babyrousa babyrussa* (L.). Skull seen from the left side. Zoöl. Mus. Buitenzorg, no. 1085. 0.5×. Original drawing by Mrs M. Idenburg in the coll. of dr K. W. Dammerman.

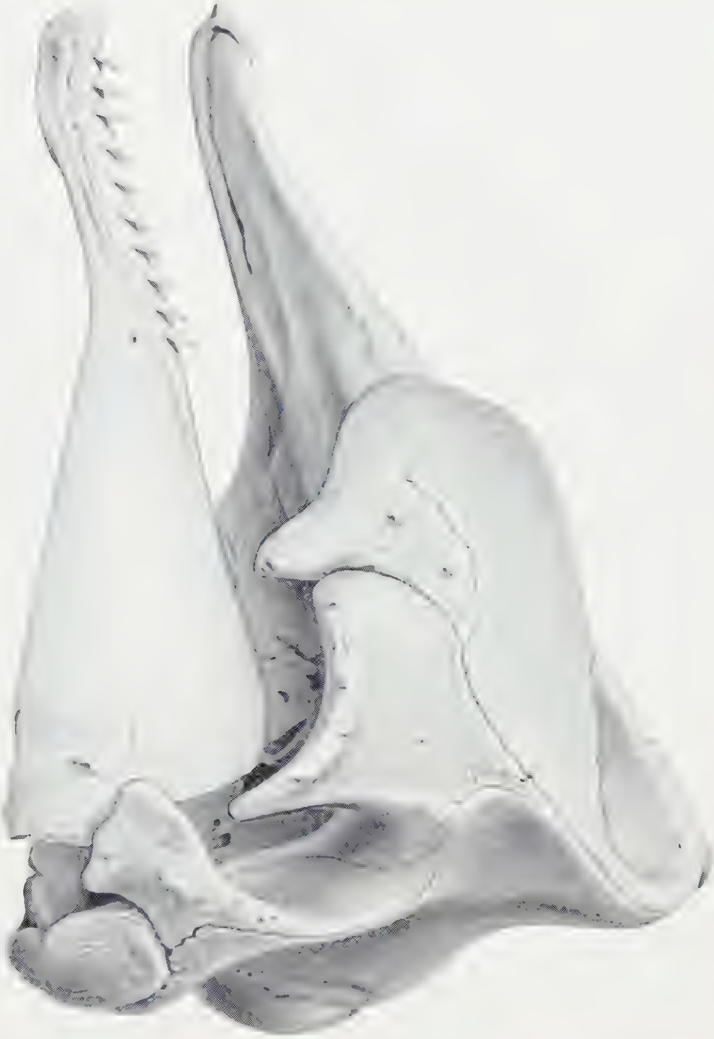


Fig. 110. *a. Kogia breviceps* (de Blainville). Skull seen from the left side. R.M.N.H. Leiden, no. 1444. 0.34×. Original drawing by M. A. Koekkoek.

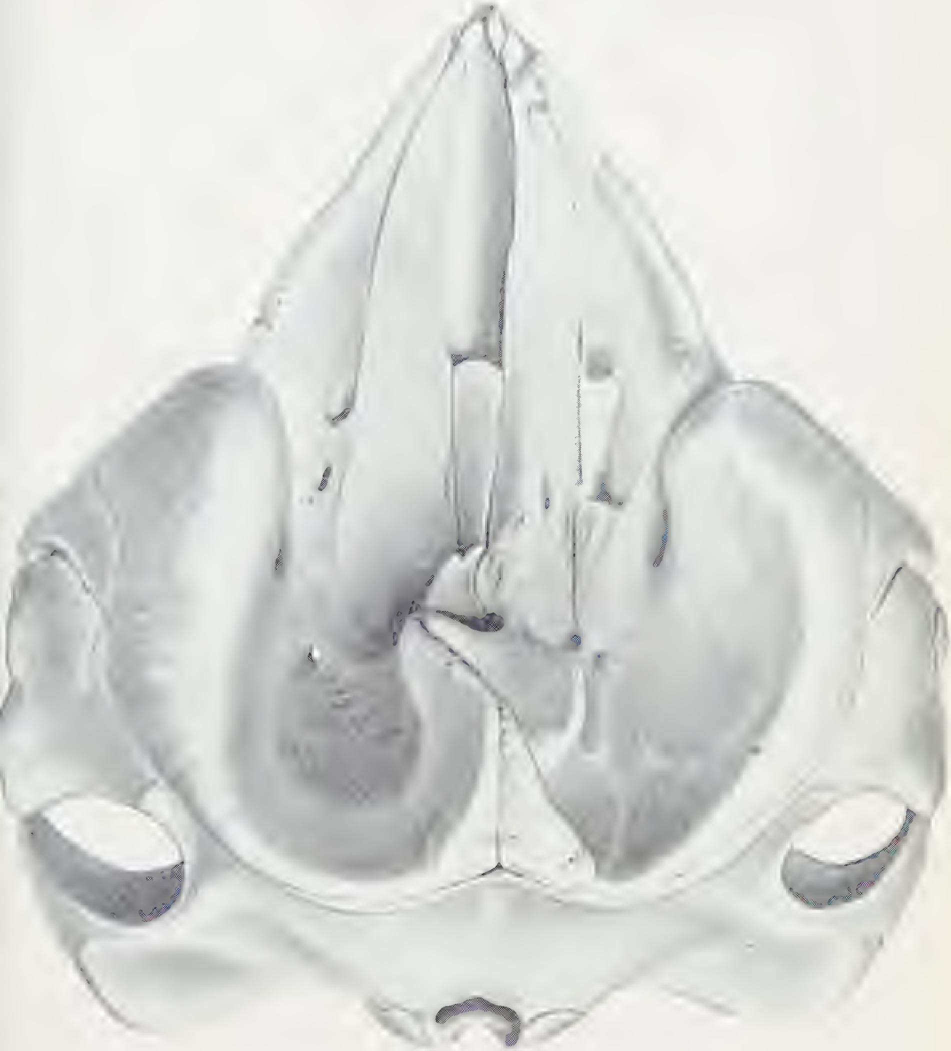


Fig. [illegible] *b*. *Kogia breviceps* (de Blainville). Skull seen from above. R.M.N.H. Leiden, no. 1444. 0.34 . Original drawing by M. A. Koekkoek.

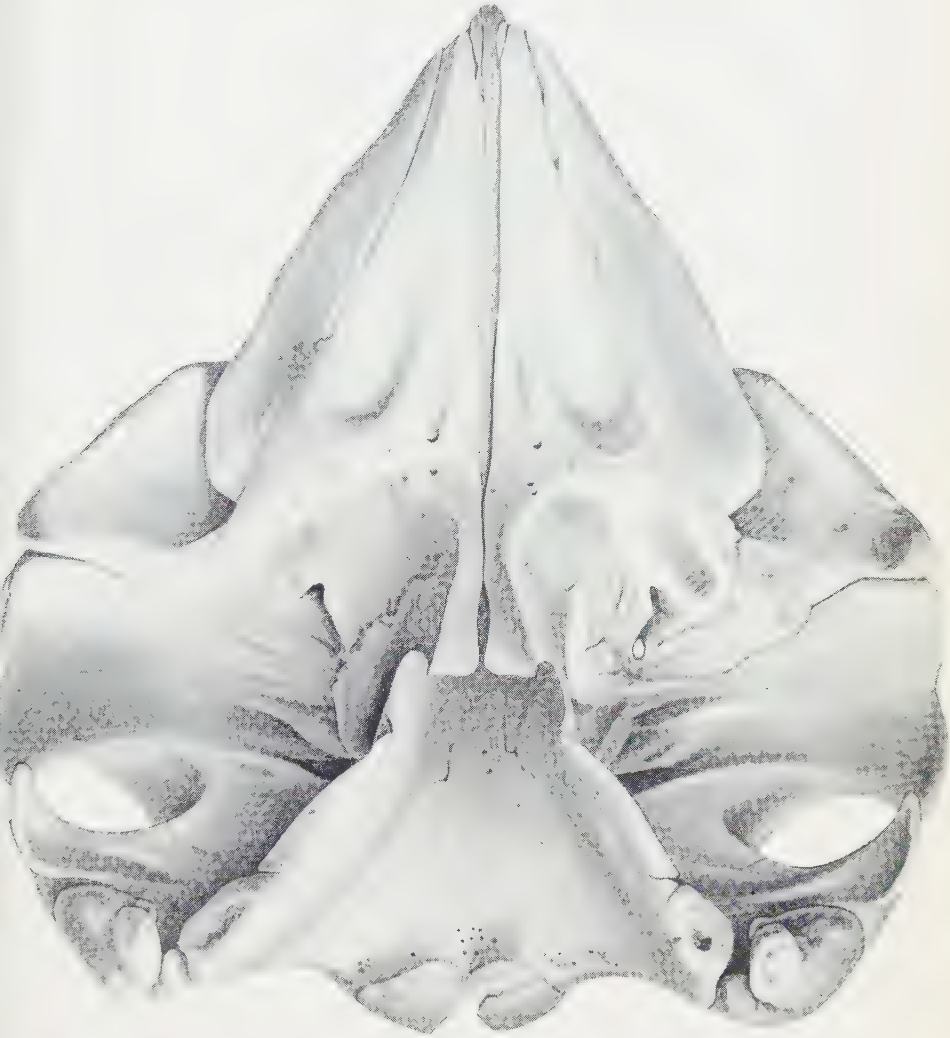


Fig. 110. *c. Kogia breviceps* (de Blainville). Skull seen from below. R.M.N.H. Leiden, no. 1444. 0.34×. Original drawing by M. A. Koekkoek.

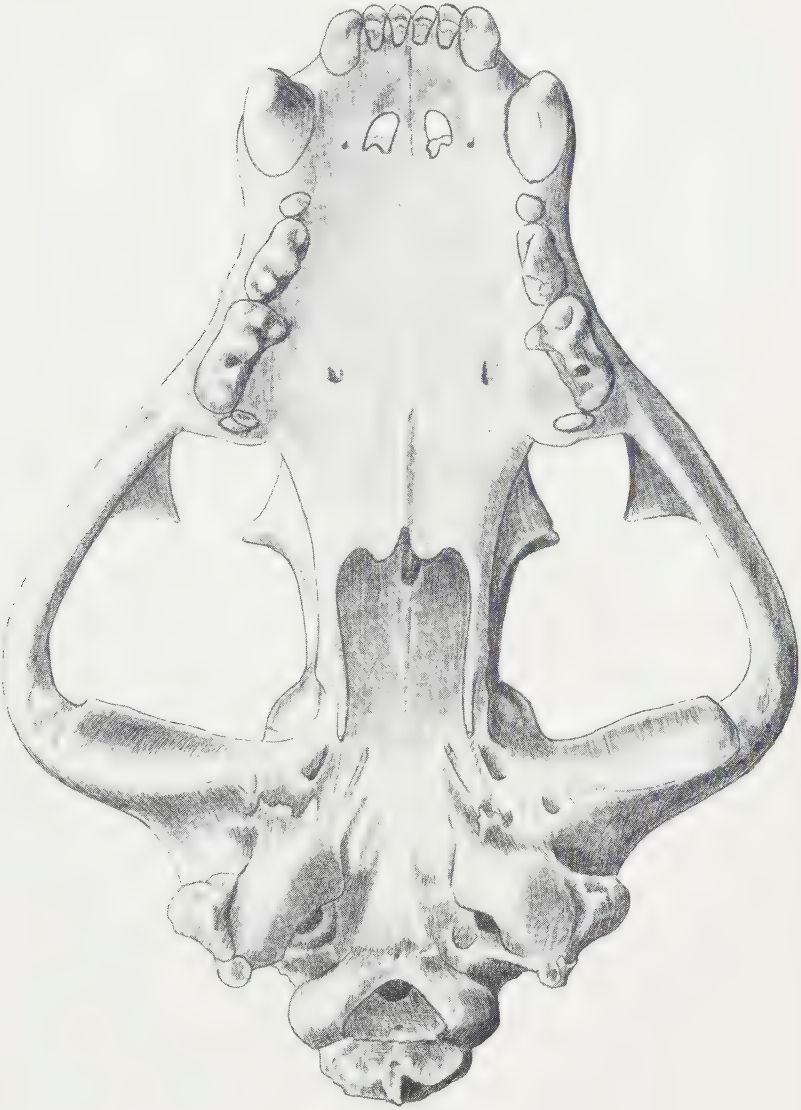


Fig. 153. *Panthera tigris* (L.). Skull seen in ventral view. Zool. Mus. Buitenzorg, no. 59/33. 0.47×. Original drawing by Mrs M. IDENBURG in the collection of dr K. W. DAMMERMAN.

SIZE AND POSITION OF THE FUNCTIONAL COMPONENTS OF THE SKULL

A CONTRIBUTION TO THE KNOWLEDGE OF THE ARCHITECTURE OF THE SKULL, BASED ON DATA IN THE LITERATURE

(Conclusion)

BY

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10-51. GENERAL REMARKS ON THE PLACES OF ATTACHMENT OF MUSCLES TO THE SKULL

The scope of the present article now demands the discussion of the functional components of the skull, determined by the places of attachment of the muscles to the skull and their part played in the architecture of the skull. We have to know absolute and relative size, shape and position of these functional components. These are three-dimensional bodies, because the attachment of muscles does not only affect the relief of the surface of the skull, to which the muscles are attached, but also the skull underneath this surface, such as the thickness of the skull, the structure of the bone in relation to lines of tension. In literature dealing with the problem of the influence of the muscles on the shape of the skull, facts about the thickness, structure a.s.o. of the bone underneath the surface to which the muscles are attached, are scarcely ever discussed, at all events not in the literature studied for this article. – Due to the influence of the attachment of muscles on the relief of the surface of the skull, this surface can show processes, crests, ridges, margins round an excavation, a certain relief of the bottom of this latter, *etc.* This relief is seldom exactly described in literature, especially in the case of the relief of an excavation. The knowledge of this, however, is valuable, as the way and the strength of the attachment is not necessarily the same all over the whole place of attachment.

The relief in general is related to the way in which the muscle is attached to the skull, as f.i. by a thin tendon, a broad aponeurosis, by a "muscular attachment" a.s.o. This in turn is related to the shape of the muscle near the place of attachment, which can be a top of a conus, a flat and thin plate, a fan, the base of a conus, *etc.*

The relief and also the structure of the bone underneath the surface of the skull, to which the muscle is attached, is also related to the strength of the muscle. As the literature studied for this article, does not discuss the relation between the strength and the size of the muscle and the development of the place of attachment of the muscle, I have not cited the data in literature on the strength and size of the muscles, though it must have a definite influence on the architecture of the skull.

There must be a relation between the development of the two places of attachment of one muscle. In the case of muscles running from the skull to parts outside the head, the architecture of the skull is influenced by these parts outside the head. In the case of muscles running from the skull to soft parts of the head, these latter influence the architecture of the skull. In muscles running from the left side of the skull to the corresponding place on the right side of the skull, these two places of attachment will be equal. In the case of muscles running from one part of the skull to another, these parts will mutually influence each other. In this latter case we can study the influence of muscles of different shape and size and strength on the places of attachment and thus on the architecture of the skull. For that practical reason I have brought the places of attachment under the following headings:

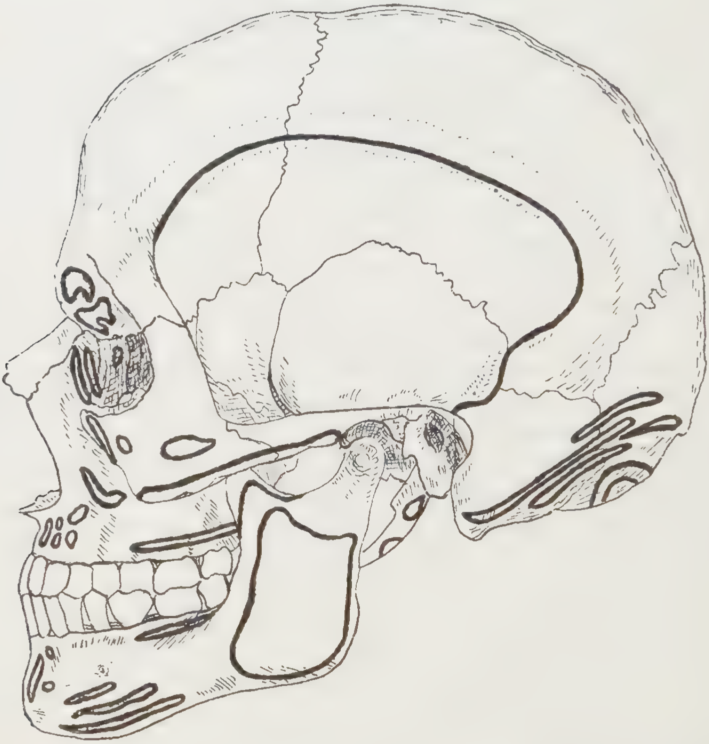

Fig. 156. *a. Homo sapiens* L. Skull with lower jaw seen from the left side, showing the outlines of the places of attachment of muscles. After Spalteholz (1919), fig. 58 on p. 45.

a) muscles which run from the skull to parts outside the head (§§ 10–22);
b) muscles which run from the skull to soft parts of the head (§§ 23–31);
c) muscles which connect corresponding skull elements of the right and left side (§§ 32–39);

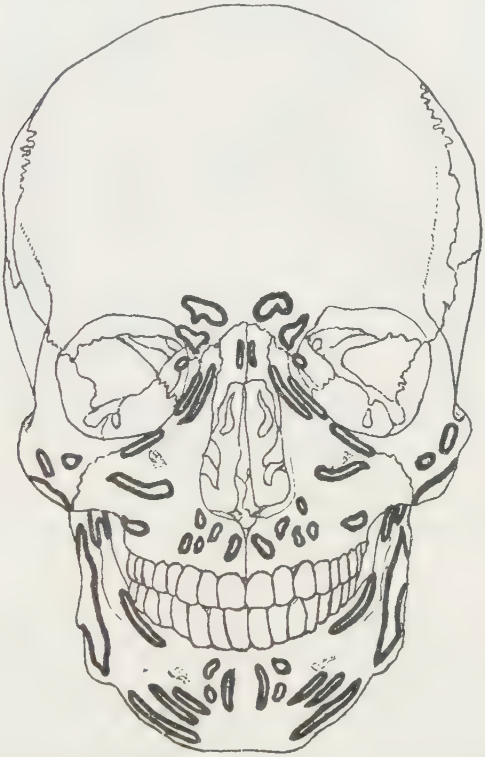

Fig. 156. *b. Homo sapiens* L. Skull with lower jaw seen in front view, showing the outlines of the places of attachment of muscles. After SPALTEHOLZ (1919), fig. 60 on p. 47.

d) muscles which run between different parts of the skull (§§ 40–51).

At the utmost literature gives the exact two-dimensional circumference of the places of attachment on the outer surface of the skull, as is known for *Homo* (see my figs 156, 157 and 158). As a rule literature only mentions the region of the skull (occiput, temporal region) or the morphological element of the skull

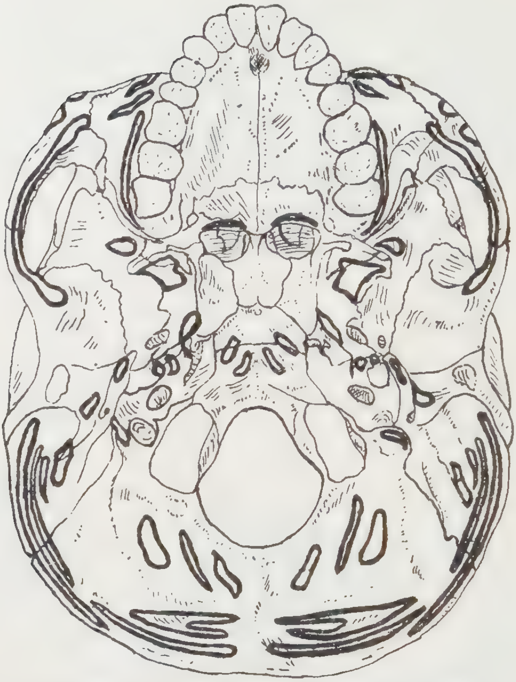

Fig. 156. *c. Homo sapiens* L. Skull without lower jaw seen in ventral view, showing the outlines of the places of attachment of muscles. After Spalteholz (1919), fig. 62 on p. 49.

(exoccipitale, squamosum), but even a special indication of the part of these regions or elements to which the muscle is attached, is no indication of the exact position nor of the exact size of this place, and not only because it gives only one dimension of this size.

Trying to interpret the relation between the size (three- and two-dimensional) and position of the places of attachment and their function one is faced with the general difficulties of the problem of the relation of form and function. Some components such as zygomatic arch, lower jaw, fulfill more than one function. A place of attachment of a muscle, as *e.g.* a processus may act as a place of attachment of more than one muscle, which in the literature on the skull are seldom mentioned with exactness, but are only indicated as "neck muscles", *etc.*

These bare facts on the places of attachment of muscles have nevertheless been collected by me. Though of little value for my

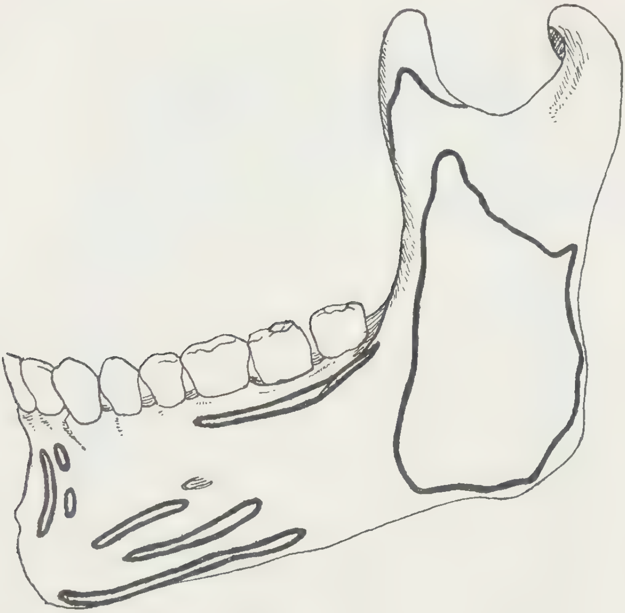

Fig. 157. *a. Homo sapiens* L. Right half of the lower jaw seen from the right side inverted, showing the outlines of the places of attachment of muscles. After SPALTEHOLZ (1919), fig. 47 on p. 38.

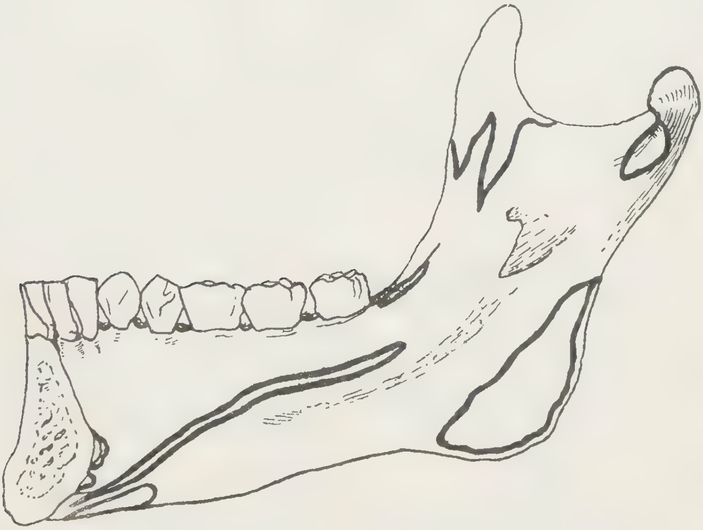

Fig. 157. *b. Homo sapiens* L. Right half of the lower jaw seen from the left side, showing the outlines of the places of attachment of muscles. After SPALTEHOLZ (1919), fig. 48 on p. 39.

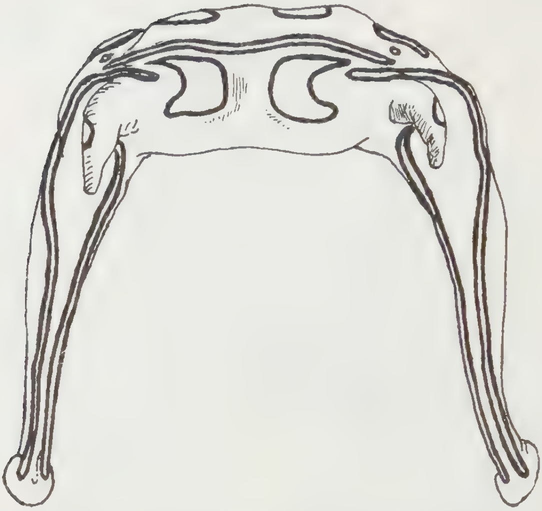

Fig. 158. *a. Homo sapiens* L. Os hyoideum seen from above, showing the outlines of the places of attachment of muscles. After Spalteholz (1919) fig. 55 on p. 43.

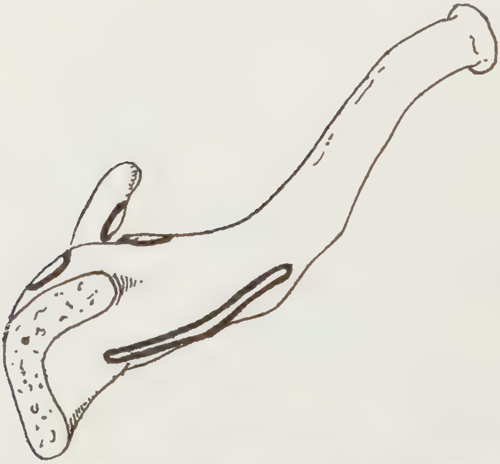

Fig. 158. *b. Homo sapiens* L. Right half of the os hyoideum seen from the left side, showing the outlines of the places of attachment of muscles. After Spalteholz (1919), fig. 56 on p. 43.

purpose at the moment, they will perhaps draw the attention of investigators to the influence of the muscles on the architecture of the skull. I have, however, limited myself to direct data on these places of attachment on the skull. I have not mentioned the cases where such direct data are lacking, but in which a homologous muscle is mentioned for a related group of animals or in which the name of the muscle seems to give an indication of the place of attachment to the skull.

In view of the general plan of this article the places of attachment of the muscles to the skull ought to be classified according to functional aspects, *i.e.* according to the function of the muscles. The literature studied for this article, limited as it was, did not allow me to do so. This literature seldom mentions the function of the muscles, does not treat the muscles according to their function, but treats them according to their homology. As the places of origin and those of insertion may vary, the function of homologous muscles may be rather different as well. Yet in a number of cases the classification of muscles according to their homology results in the grouping together of muscles with the same function and with the same places of attachment.

Based on the division of the muscles from a morphological point of view, I have tried to catalogue the places of attachment of the muscles on the skull in a kind of practical scheme to make the survey of the numerous places of attachment of the numerous muscles a little easier. Starting from this practical point of view we get a division of the muscles in a kind of natural grouping of the muscles. As mentioned above these groups of muscles are brought under the four headings according to their places of attachment.

10–22. PLACES OF ATTACHMENT OF MUSCLES RUNNING FROM THE SKULL TO PARTS OUTSIDE THE HEAD

Under this heading belong only the places of attachment of muscles of the so-called trunk musculature, with the exception, however, of the epibranchial musculature.

10. PLACES OF ATTACHMENT OF THE GENERAL TRUNK MUSCULATURE IN MARSIPOBRANCHII

The position

The following places of attachment are mentioned.

Trabecula: insertion of the musculus supraocularis (that is the dorsal part of the cranial myomere of the two prebranchial myomeres of the trunk musculature) in adult Petromyzonidae (Nishi, 1938, p. 354).

Capsula nasalis: to it partly adjoins the small dorsal or supraocular part of the first cranial myomere of the trunk musculature in *Bdellostoma* (Nishi, 1938, p. 356); to it partly adjoins cranialwards the dorsal myomere (that is the dorsal part of the first myomere) in *Myxine* (Nishi, 1938, p. 357).

Cartilago annularis: on its lateral surface insertion of the musculus subocularis or the so-called facial myomere in adult Petromyzonidae (Nishi, 1938, p. 355).

Hyoid: on the so-called hyoid insertion of the musculus rectus abdominis in Myxinidae (Nishi, 1938, p. 357).

11. PLACES OF ATTACHMENT OF THE DORSAL TRUNK MUSCULATURE

a. Introduction

The general statement that the dorsal trunk musculature in Pisces shows a place of attachment to the skull takes no account of the innervation of the muscles and so is of little value in modern literature (Nishi, 1938, p. 361). Seeing that a great part of the publications, modern ones included, on the skull do not take this into account, and often mention "trunk muscles" without any addition, the only thing left to us appears to be to mention such data from literature without the desirable precision. It is not even possible here to separate "trunk muscles" from "neck and throat muscles" if we speak only of "trunk muscles" and "neck muscles". Therefore part of these data should, perhaps, be given under § 16.

b. The size of the places of attachment

It may, in general, be supposed that the data in the literature on the size of the places of origin of neck and trunk muscles, refer to data on their relative size.

In stages of development

In Pisces crests and ridges do not appear until the related muscles are well developed; they appear as growth proceeds, in late fry and immature stages as the muscles increase in strength (Gregory, 1933, pp. 327, 443, 445).

In adult animals

In Pisces

In *Tarpon atlanticus* (C. & V.) the posttemporal fossae or fenestrae, through which a.o. the dorsal muscles of the flanks or spinal muscles pass and thus pass beneath the dermal skull roof, are large and the posterior end of the thin skull roof, lining the space wherein these muscles are situated, is lifted high above the level of the brain tube (GREGORY, 1933, pp. 139, 243).

In *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi* Clark) the body musculature evidently did not extend forward and there is no ordinary extension of the dorsal axial muscles above the occiput, there being no posttemporal fossae and no longitudinal crests on top of the cranium (GREGORY, 1933, p. 178).

We find many data on the size, the length as well as the breadth of the longitudinal crest on top of the cranium in the sagittal plane. The function of this crest in the attachment of the muscles is, however, not always given, and the muscles themselves are hardly ever mentioned.

The occipital crest in *Antigonia capros* Lowe shows an excessive height, in which regard *Antigonia capros* Lowe is more specialized than *Capros aper* (L.) (GREGORY, 1933, p. 273).

In *Scorpis georgianus* C.V. the dorsal crest does not protrude very far, in connection with the fact that the muscle area does not extend forward on the forehead (GREGORY, 1933, pp. 274/275, fig. 150).

In *Monodactylus* (*Psettus*) the supraoccipital crest is produced forward, its anterior rim being inclined above the frontalia (GREGORY, 1933, p. 275).

In *Chaetodon* the supraoccipital crest is extremely high (GREGORY, 1933, p. 279, fig. 155).

In *Lampris luna* (Gmel.) there is a huge sagittal crest on the supraoccipitale and frontalia which extends forward above the praefrontalia (GREGORY, 1933, p. 296, fig. 174). In *Velifer* the sagittal crest is much higher, while in *Trachypterus* the occipital crest has disappeared (GREGORY, 1933, pp. 297, 299, fig. 173).

All Carangidae have a conspicuous extension of the sagittal crest from the supraoccipitale to the frontale, which is higher and steeper in the more primitive compressed types and lower and more elongate antero-posteriorly in the derived long-bodied types (GREGORY, 1933, p. 302).

Coryphaena has a distally developed sagittal crest (GREGORY, 1933, p. 305, fig. 183).

In Scombroidei the occipital crest is low and extends forward over the frontalia to the ethmoid (GREGORY, 1933, p. 310, fig. 189). In many Scombroidei, such as *Coryphaena hippuris* L. and *Thunnus*, the supraoccipital crest extends forward to the snout and is supported by a great horizontal plate formed by the frontalia (GREGORY, 1933, p. 437, figs 183, 192).

In *Luvarus* the skull roof is depressed to the plane of the vertebral column by the steeply developed epaxial muscles which extend forward to the ethmoid, forming a high crest (GREGORY, 1933, p. 306, fig. 185).

Referring to the condition in *Symbranchus*, where two wide flat parietalia meet in the mid-line above the minute supraoccipitale, GREGORY (1933, p. 352) mentions that this arrangement, as in so many other cases, appears to be correlated with a long flat-topped skull in which the axial muscles do not extend on top of the occiput.

Apart from the crest in the median line which may extend forward to a greater or lesser degree, there may be other crests and ridges connected with the attachment of trunk muscles.

In *Luciolates* the anterior prolongations of the spinal muscles in the occipital region pass above the dermal skull roof between long and well-braced ridges (GREGORY, 1933, pp. 242/243, fig. 117). One of them is a high crest on the parietale that divides the trunk muscles of *Luciolates* into one lower and two upper strands (p. 244).

In *Balistes*, where the eye is situated very far back, we find heavy ridges above and behind the eyes and on the occipital surface for the insertion of the dorsolateral muscle and the deep vertebral muscles (GREGORY, 1933, pp. 285/286).

In Scombroidei we find, by the side of the occipital crest, parallel and continuous crests on either side, which run forward from the epioticum over the parietalia on to the frontalia (GREGORY, 1933, p. 310, fig. 189).

In Amniota in general

In Amniota we see clearly that the size and development of the place of attachment of the neck muscles depends on the development of these muscles (VERSLUYS, 1936, p. 741). The development of the neck muscles depends on the weight of the head and skull, and this is again connected indirectly with the length of the neck. However, it is also connected with the size of the animal (STADTMÜLLER, 1936, pp. 951/952), with the position of the axis of the skull with regard to the axis of the vertebral column, and so, indirectly, with the position of the foramen magnum.

In Reptilia

In Reptilia we see that the neck muscles influence those cranial elements to which they are attached (VERSLUYS, 1936, p. 741). Thus in Reptilia there is correlation between the relative length of the neck muscles and the shape of the occiput (VERSLUYS, 1936, p. 741).

The development of the tuberculum sphenoccipitale in Reptilia depends on the development of the ventral neck muscles which are attached to it (VERSLUYS, 1936, p. 741).

In fossil Sauria with their long necks, as in *Camelus*, *Giraffa*, *etc.*, among Mammalia, the possibilities for insertion and origin of the enlarged masses of muscle where the relation-complex has been summarized in the so-called Law of BERGMANN, have better chance of realisation than in a short cervical vertebral column (STADTMÜLLER, 1936, p. 952).

I have not been able to find particulars as to the size and development of the places of attachment in †Rhamphorhynchoidea and in †Pterodactyloidea in the literature I consulted. We may expect here a solution identical to that in Aves, where the development of the places of attachment differs in birds of the straight skull type and those of the skull type with a curved or cracked longitudinal axis. In connection with what we shall see in the discussion of these matters in Aves, we want to point out here that in †Rhamphorhynchoidea and in †Pterodactyloidea the elongated snout is very light owing to the large nostrils and the fenestrae praeorbitales (VERSLUYS, 1936, p. 797).

In Aves

In Aves we find that the neck muscles are very heavily taxed in the straight type of skull, because the centre of gravity of the skull lies very far rostralward before the occipital joint and the cervical vertebral column attaches itself to the occiput in line with the axis bill—skull base. The planum occipitale shows clear places of attachment for the neck muscles, sometimes even knobs and crests. The planum occipitale is clearly separated from the roof of the skull and from the fossae temporales here present, which latter are made clearly visible by sharp-edged crests.–In the type of skull with a curved or cracked longitudinal axis, the neck muscles are, to a high degree, relieved, because the centre of gravity of the skull lies above the occipital joint, the cervical vertebral column is attached to the ventral side of the cerebral skull, while at the same time the bill does not protrude very far because of its curve (MARINELLI, 1936, pp. 811/812, 817/818, 822, 834).

Especially in heavy skulls and in skulls heavily burdened in front we find outside on the bottom of the cerebral skull high muscular protuberances and grooves, such as is the case in Bucerotidae (MARINELLI, 1936, p. 814). As a rule, however, the upper bill is very lightly built because the skeleton has been reduced to a construction of rods and because the outer nostrils and the fenestra antorbitalis are very large.

In Picidae where the bill is used as a hammer and the skull must be very firmly attached to the cervical vertebral column we find a protruding crest for the neck musculature on the occiput (BÖKER, 1937, p. 30).

In Mammalia

In Mammalia the neck muscles may attach themselves to a smooth surface of the cerebral skull, but it is possible for crests and ridges to occur on the outer surface of the cerebral skull (STADTMÜLLER, 1936, p. 911).

In short-necked Mammalia, such as *Elephas*, the skull, or rather the plane of attachment of the neck muscles on the skull, must be considerably enlarged in order to offer large planes of attachment to these muscles, according to STADTMÜLLER (1936, p. 952). This enlargement of the skull surface is brought about by crests, ridges, *etc.*, or by the outer surface of the skull being situated at a clear distance from the cerebral capsule and the space between is filled by a spongy bone formation.

In long-necked Mammalia, such as *Camelus*, *Giraffa*, *etc.*, the possibilities for insertion and origin of the enlarged masses of muscle which relation-complex has been summarized in the so-called Law of BERGMANN, have better chance of realisation than in a short cervical vertebral column according to STADTMÜLLER (1936, p. 952).

Elephas on the one hand and *Camelus* and *Giraffa* on the other, given above as examples, are, however, extremes. It would be interesting to trace how conditions are in the intermediary stages. BÖKER (1937, pp. 112/113) gives as a series with increasing neck length: *Elephas*, *Bos taurus* L., *Equus caballus* L. and *Camelus*.

MARINELLI (1929, pp. 128–132) goes much deeper into the factors influencing in Mammalia a powerful or weak development of the places of attachment of the neck muscles. MARINELLI traces the connection with the manner in which the head as a whole is carried and moved as a weapon, as a tool, *etc.*

Of primary importance is here the neck type, *i.e.* if the longitudinal axis of the skull lies in the produced part of the cervical vertebral column, as also occurs in Pisces, or, whether the cervical vertebral column runs perpendicularly from the axis of the skull or forms an angle with it.

In the second place it is of importance how the centre of gravity of the skull is situated with regard to the point of support, *i.e.* the occipital joint, whether it is situated close to it, as is the case in Carnivora (the head being used as a dagger, the prey is hurt and mastered, the sharp or pointed seizing-teeth are sure of their aim and are worked with the swiftness of a flash of lightning) or, whether the centre of gravity is, horizontally, very far from the occipital joint as is the case in *Rhinoceros* and also in †Titanotheria (in its function as a weapon the head is used as a club, the other animal is wounded and overpowered by the force of the collision).

In the third place the carriage of the head is important in this respect: whether the centre of gravity of the head is vertically low with regard to the occipital joint (the head hangs) or whether it is high with regard to this point of support of the skull (the head is carried high).

Where the neck type is carrying, where the longitudinal axis of the skull does not lie in the produced part of the cervical vertebral column, but the cervical vertebral column is nearly at right angles to the skull, so that it is at right angles to the skull base, we must distinguish two extremes with regard to the position, horizontally measured, of the centre of gravity of the skull, *viz.* the bullet-shaped skull and the elongated skull.

In the bullet-shaped skull, such as occurs in *Homo*, where the development of the cerebral capsule is decisive for the shape of the skull, the skull rests on the vertebral column and the neck muscles are poorly developed.

In the elongated skull, which is normal in the carrying neck type, the centre of gravity of the skull lies, horizontally measured, at a clear or even great distance from the point of support of the skull. As examples MARINELLI mentions: *Camelus*, *Cervus* and *Equus caballus* L. In these cases we may speak of a "square lever", wherein the lever of load is formed by the skull base (basioccipitale and basisphenoid) and the lever of force is formed by the caudal wall of the occiput. The angle between these two levers is fixed by the bones in the otic region and the squamosum. The gyratory moment thus formed must be counteracted by the neck muscles. Part of these muscles is attached to the neck, part to the trunk. On the other side these muscles attach themselves to the upper side and the outer plane of the, in these cases very thick, occipital wall. In such skulls the lateral wings of the os sphenoideum are very strongly developed; they connect the strongly developed skull base with the strongly protruding facial skull and they prevent this latter from bending downward and caudalward. Consequently, many lines of pressure, coming from different directions converge in the body of the os sphenoideum (somewhere else we shall see that the lateral wings of the os sphenoideum also play a part in the attachment of the back-teeth in the upper jaw). The development of the plane of attachment of the neck muscles of this type of skull discussed just now, is also influenced by the fact whether the head is carried high or hanging. In *Equus caballus* L. *e.g.* the very long and stretched head is carried hanging down, *i.e.* the centre of gravity of the skull lies low with regard to the occipital joint.

Opposed to the carrying type of neck is the hanging type, where the entire skull is kept "floating" mainly by the neck muscles and where the entire skull is principally hung up to those muscles which are generally supported by a powerful ligamentum nuchae. The longitudinal axis of the skull lies in line with the cervical vertebral column and the skull base too. Consequently there is no "square lever" as in the carrying neck type. Therefore the neck muscles need not counteract a gyratory moment and, consequently, they are comparatively poorly developed. The short head muscles running to the first two cervical vertebrae are comparatively poorly developed in *Bos taurus* L., which MARINELLI discusses as an example (according to him the skull of the *Bison* is the best example of this hanging neck type). Consequently the occipital plane of the skull of *Bos taurus* L. is considerably weaker in development than in *Camelus*, *Cervus* and *Equus caballus* L. Yet the carriage of the head is the same in

Bos taurus L. and in *Equus caballus* L.: hanging, in the sense that the centre of gravity of the skull lies low with regard to the occipital joint (MARINELLI, 1929, p. 131). Somewhere else, however, MARINELLI (p. 131) says that there are also Cavicornia that carry their heads "high". In the skulls of this hanging neck type the lateral wings of the os sphenoideum are of little importance; in *Bos taurus* L. they are paper thin. To this we may add that, according to MARINELLI (1929, p. 132), not only in Mammalia but also in Reptilia the basisphenoid is, so to say, a junction of the entire structure. The powerful development in *Varanus*, where the processus basipterygoidei have the same function as the lateral wings of the os sphenoideum of Mammalia, points to this.

When considering the strength of the development of the plane of attachment of the neck muscles to the occiput of the skull, we shall do well to remember, like MARINELLI (1929, p. 132), that these constructions depending on the way in which the head is carried, only appear clearly in very heavy skulls. The less heavy skulls are, owing to the demands made on their solidity by the other functions of the skull, powerful enough.

I do not know if the exceptional strong musculature running from the cervical vertebral column to the skull base in digging Mammalia such as *Talpa*, *Condylura*, *Chrysochloris*, *Notoryctes*, *Geomys*, *etc.* (BÖKER, 1935, p. 175), leads to a certain development of this place of attachment on the skull base.

c. The position

The position of the places of attachment of the neck and trunk muscles naturally followed the discussion of other things in the above, so that a separate discussion of the position would only be a repetition of what has just been said. Therefore we only want to add the following.

In Pisces

In *Astroscopus y-graecum* (C.V.) the broad flat occiput evidently afforded insertion for thick axial muscles (GREGORY, 1933, p. 370). In the Gastrostomidae the very thick neck and back muscles are attached to the remarkably wide and short neurocranium (GREGORY, 1933, p. 438). No mention is made of crests or ridges.

In Crossopterygii the fossa subchordalis, which is situated in the otical and occipital part of the skull base, was, in all probability, mainly filled by part of the trunk musculature (Holmgren & Stensiö, 1936, p. 351).

In Amphibia

Occipitale laterale: insertion of the musculus vertebrocapitis profundus in Caudata, separate attachment of the musculus intertransversarius capitis (that is a small ventral part of this muscle), lacking in *Necturus* and *Proteus* (Nishi, 1938, p. 378); insertion of the musculus intertransversarius capitis dorsalis (that is the first cranial portion of the musculus dorsalis trunci *s.* musculus longissimus dorsi) in Salientia (Nishi, 1938, p. 379).

Squamosum: insertion of the musculus vertebrocapitis superficialis in Caudata (Nishi, 1938, p. 378).

In Reptilia

Skull (without detailed indication): insertion of the musculus testotransversalis capitis *s.* testocapitis lateralis in Testudinides, feebly developed or lacking in some of them (Nishi, 1938, p. 390); insertion of the musculus testospinalis capitis *s.* testocapitis medius in Testudinides, lacking in some groups of them (Nishi, 1938, pp. 390/391); insertion of the musculus spinalis capitis *s.* cervicocapitis medius in Testudinides (Nishi, 1938, p. 391).

Dorsal surface of the skull: on this the very powerful neck muscles overlap in Amphisbaenidae (Versluys, 1936, p. 741).

Occipitale basilare: insertion of the musculus iliocostalis in Serpentes (Nishi, 1938, p. 389).

Occipitale laterale: insertion of the musculus longissimus capitis profundus in Loricata (Nishi, 1938, pp. 387, 393); till it can be followed the musculus iliocostalis cervicis *s.* cervicocapitis *s.* cervicalis ascendens in a number of genera of Sauria (Nishi, 1938, pp. 389, 393); attachment of a small muscle belonging to this system in Chamaeleontidae, in which the former muscle does not run so far rostralwards (Nishi, 1938, p. 389); till it may in some cases be followed the musculi articulotransversarii as musculi transversales capitis in Testudinides (Nishi, 1938, p. 390).

Supraoccipitale: insertion of the musculus spinalis capitis (that is the cranial prolongation of the musculus articulospinalis) in Serpentes (Nishi, 1938, pp. 390, 393).

Processus occipitalis: attachment of ventral neck muscles in part of the Reptilia (Versluys, 1936, p. 741).

Tuberculum sphenoccipitale: attachment of ventral neck muscles in part of the Reptilia (Versluys, 1936, p. 741).

Tuberculum sphenoticum: insertion of the musculus transversalis cervicis (that is the deeper, more or less isolated part of the musculus longissimus cervicocapitis) in Rhynchocephalia (Nishi, 1938, p. 388).

Opisthoticum: partial insertion of the musculus longissimus cervicocapitis in Rhynchocephalia (Nishi, 1938, p. 388).

Squamosum: insertion of the musculus longissimus capitis superficialis in Loricata (Nishi, 1938, pp. 387, 393); also insertion of another muscle, perhaps the musculus collosquamosus, in Loricata (Nishi, 1938, p. 387); partial insertion of the musculus longissimus cervicocapitis in Rhynchocephalia (Nishi, 1938, p. 388); insertion of the musculus collosquamosus in Testudinides (Nishi, 1938, p. 390); attachment of "neck muscles" in †Phytosauria (Parasuchia) (Versluys, 1936, p. 741).

Postparietale, parietale and posttemporal arch: on the caudal margin of these elements attachment laterally of the musculus longissimus capitis superficialis and medially of the musculus transversospinalis capitis in Reptilia (Versluys, 1936, p. 741).

Parietale: partial insertion of the musculus longissimus cervicocapitis in Rhynchocephalia (Nishi, 1938, p. 388); on its caudal margin inserts the musculus spinoparietalis *s.* spino-occipitalis *s.* semispinalis capitis in Rhynchocephalia (Nishi, 1938, p. 388); to it ascends the musculus longissimus capitis in Serpentes (Nishi, 1938, pp. 389/390).

In Aves

Occiput (without detailed indication): insertion of the dorsal part of the musculus longissimus capitis superficialis *s.* complexus major (Nishi, 1938, p. 391); insertion of the musculus spinalis capitis, which is seldom lacking (Nishi, 1938, p. 392).

Occipitale laterale: insertion of the musculi transversales capitis (Nishi, 1938, p. 391).

Squamosum: insertion of the lateral part of the musculus longissimus capitis superficialis *s.* rectus capitis anterior lateralis (Nishi, 1938, p. 391).

In Mammalia

Occiput (without detailed indication): insertion of the musculus transverso-occipitalis *s.* semispinalis capitis, more or less divided into two parts (biventer cervicis and complexus major) (Nishi, 1938, p. 408); insertion of the musculus rectus capitis dorsalis major, often divided into a superficial and into a deep layer (Carnivora, Marsupialia), seldom into a lateral and into a medial part (*Sus*, *Elephas*) (Nishi, 1938, p. 409); insertion of the musculus rectus capitis dorsalis minor, which may be absent (*Putorius*), or double (*Ursus*), or fused with the musculus rectus capitis dorsalis major (*Kogia*, *Trichechus* (*Manatus*)) (Nishi, 1938, p. 409); insertion of the musculus obliquus capitis, which is lacking in Monotremata, Didelphyidae, *Chlamydophorus* and *Dasypus*, is double in *Marmota* (*Arctomys*), *Meles*, *Elephas* and *Phascolarctos* (Nishi, 1938, p. 409).

Occipitale laterale: towards it extends the musculus longissimus in Cetacea and Sirenia (Nishi, 1938, p. 408).

Processus mastoides: insertion of the musculus longissimus cervicis et capitis *s.* transversalis cervicis et capitis *s.* complexus minor (Nishi, 1938, pp. 407/408); insertion of the musculus splenius capitis, which is lacking in *Trichechus* (*Manatus*) (Nishi, 1938, p. 408).

12. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE DORSAL FINS IN PISCES

a. Introduction

We shall also discuss here the attachment of the muscles of the illicium, originating from the cephalic extensions of the dorsal fin (the second and third rays of the spinous dorsal), found in Pediculati. The discussion of the attachment of these muscles cannot be separated from that of the insertion of the illicium itself on the dorsal side of the skull. Therefore we shall discuss this insertion in the following lines, without devoting a separate chapter to it.

b. The size of the place of attachment of the muscles and of that of the illicium

For Pisces in general Gregory (1933, p. 437) mentions that the supraoccipital crest supports the anterior extensions of the muscles of the dorsal fins.

The nuchal fin muscles in *Capros aper* (L.) are limited anteriorly by a sharp ridge on the supraoccipital crest, which curves downward and is continuous with a curved crest on the frontale and epioticum (Gregory, 1933, p. 273, fig. 149A).

In *Monodactylus* (*Psettus*) we find by the side of the supraoccipital crest also paired median crests which the frontalia send up to meet the supraoccipital crest. The cranial roof thus forms a platfrom for the nuchal fin muscles as in *Brama*, *Coryphaena* and *Velifer* (Gregory, 1933, p. 275).

In the Veliferidae and the Trachypteridae there is a large chamber on the anterior part of the cranium, the walls formed by the frontalia, the floor partly by the mesethmoid. This chamber is absent in the other families of the order to which these families belong. In *Lampris* the median cavity between the frontal flanges has disappeared. It need hardly be said that the laterodorsal surfaces of the frontal flanges serve as a base for forwardly produced muscles of the nuchal crest, Gregory (1933, pp. 297/298) says.

In *Antennarius* and its allies the enlargement of the basal muscles of the second and third rays of the spinous dorsal may have initiated the enlargement of the supraoccipital and the median depression formed by the supraoccipitale and the frontalia, the so-called illicial trough, is more or less filled by the basal rods of the second and third dorsal rays and the muscles attached on them (Gregory, 1933, pp. 391, 392, 403, fig. 265B).

In the Ceratioidae the illicial trough forms a prominent feature; it represents a caving-in of the skull roof due to the presence of the enlarged basal bone of the illicium and of the usually strong muscles, arranged in three pairs, which are attached to it. In the more advanced Ceratioidae, such as the Ceratiidae, this trough forms a deep groove extending backwards on the roof of the occiput and lying between the raised epiotica (GREGORY, 1933, p. 403).

In Oneirodidae the illicial trough extends along the whole length of the upper surface of the skull (GREGORY, 1933, p. 404).

In Gigantactidae the enormously elongated illicium is supported by enlarged mesethmoid and lateral ethmoids (GREGORY, 1933, p. 404).

c. The position

Many data may be derived from the above. To those is added as place of attachment:

Occiput: the origin of the musculus supracarinalis cranialis or musculus levator *s.* protractor pinnae dorsalis (NISHI, 1938, p. 373).

As regards the position of the illicium we may add the following.

In the Ogcocephalidae we find reduction of the illicium and a forward displacement of the illicial fossa beneath the newly formed rostrum (GREGORY, 1933, p. 398). In *Ogcocephalus vespertilio* (L.) where we find a shrinking of the illicium, there is a median interorbital and supra-ethmoidal fossa (GREGORY, 1933, p. 397). In *Chaunax coloratus* Garman the illicium is received into a fossa in the ethmoid region (GREGORY, 1933, p. 401).

13. PLACES OF ATTACHMENT OF THE ABDOMINAL MUSCULATURE IN ANAMNIA

The position

In Pisces

Neurocranial base: on the ventral side of the skull insertion of the musculus obliquus superior or rather the musculus obliquus dorsalis in Selachii (NISHI, 1938, p. 362).

Lower jaw: on its ventral margin insertion of the musculus rectus externus in *Lepidosiren* and in *Protopterus* (NISHI, 1938, p. 366).

Hyoid: on the hyoid copula and on the adjoining part of the hyoid arch attachment of the deep portion of the musculus rectus together with the musculus obliquus internus in Dipneusta (NISHI, 1938, p. 366); on the powerful hyoid arch partial insertion of the musculus rectus internus with the musculus obliquus internus in *Lepidosiren* and *Protopterus* (NISHI, 1938, p. 366).

Branchial arches: partial insertion of the musculus rectus internus with the musculus obliquus internus in *Lepidosiren* and *Protopterus* (NISHI, 1938, p. 366).

In Amphibia

Skull (without detailed indication): towards it extends the musculus longus capitis et colli *s.* flexor colli et capitis *s.* praevertebralis ventralis in Apoda (Nishi, 1938, p. 382).

Occiput: on it the musculus subvertebralis in Caudata begins (Nishi, 1938, p. 380); the musculus intertransversarius ventralis *s.* praevertebralis dorsalis is said not to extend so far as that in Apoda (Nishi, 1938, p. 382).

Occipitale laterale: this is reached by the musculus cervicalis lateralis *s.* costocervicalis in Caudata (Nishi, 1938, p. 380); attachment of the musculus rectus capitis lateralis *s.* intertransversarius capitis ventralis in Salientia (Nishi, 1938, p. 381).

Tongue bone: origin of the musculus hyoabdominalis in *Breviceps* (Nishi, 1938, p. 381).

Larynx: attachment of the cranial fascicles of the musculus transversus in Salientia (Nishi, 1938, p. 381).

14. PLACES OF ATTACHMENT OF THE HYPOBRANCHIAL MUSCULATURE IN ANAMNIA

The position

In Pisces

Skull (without detailed indication): to it are sent stray fibres of the most caudal musculus pharyngoclavicularis in Dipneusta (Nishi, 1938, p. 371).

Labial cartilages: to the upper labial cartilage-apparatus run the lateral parts of a smaller muscular fascicle, which is part of the musculus coracomandibularis and which is connected with the muscle-tracts of the constrictor system, in *Callorhynchus*, while to the medial connections of the two lateral premandibular cartilages the middle section of it can be followed as the musculus coracopraemandibularis in *Callorhynchus* (Nishi, 1938, pp. 369/370).

Lower jaw: insertion of the musculus coracomandibularis (Nishi, 1938, pp. 369, 371); mostly on the middle of the united mandibulae as an unpaired muscle in Squaliformes, in which the muscle is feebly developed or sometimes is lacking (Nishi, 1938, p. 369); in *Lepisosteus* and in Teleostei this muscle is lacking (Nishi, 1938, p. 370).

Hyoid: insertion of the musculus coracohyoideus (Nishi, 1938, pp. 369, 371); mostly on the copula of the hyoid as an unpaired muscle in Squaliformes (Nishi, 1938, p. 369); on the urohyale insertion of the musculus coracohyoideus *s.* cleidohyoideus *s.* sternohyoideus as one single muscular conus in Teleostei (Nishi, 1938, p. 370); on the basihyale, on the connecting place of basi- and ceratohyale, on the hypohyale and on the adjoining end of the ceratohyale insertion of the three tracts of the musculus coracocleidohyoideus in *Neoceratodus* (Nishi, 1938, p. 371); on the ceratohyale insertion of the musculus coracocleidothoracohyoideus in *Protopterus* and in *Lepidosiren* (Nishi, 1938, p. 371).

Branchial arches: on their ventral parts insertion of the musculi coracobranchiales (Nishi, 1938, pp. 369, 371); on the ventral parts insertion of the same number of musculi coracobranchiales in Squaliformes (Nishi, 1938, p. 369); on the strongly developed ceratobranchiale V and in some species of Batoidei even on the epibranchiale V (here a musculus coracobranchialis 5 dorsalis and ventralis may be distinguished) insertion of the strongly developed musculus coracobranchialis 5, being part of the system of five musculi coracobranchiales, which are mainly fused to one single muscle, the musculus coracobranchialis 1 being a musculus coracohyomandibularis (Nishi, 1938, p. 369); on the branchial arches II–V insertion of the musculi pharyngoclaviculares in Dipneusta, in which the musculi coracobranchiales are lacking (Nishi, 1938, p. 371).

In Amphibia

Tongue bone: mainly on the corpus of the tongue bone and on the urobranchiale partial attachment of the musculus sternohyoideus in Caudata (Nishi, 1938, p. 383); on the cranial horn of the tongue bone origin of the musculus cornuoideus posterior and on the caudal horn of the tongue bone attachment of the musculus sternocornuoideus in *Uperodon* (*Cacopus*) (Nishi, 1938, p. 383).

Branchial arches: on the copula of the arcus branchialis I or II partial attachment of the musculus sternohyoideus in Caudata (Nishi, 1938, p. 383); on the arci branchiales insertion of the deeper fascicles of the musculus sternohyoideus *s.* thoracicohyoideus in Apoda (Nishi, 1938, p. 384).

15. PLACES OF ATTACHMENT OF THE VENTRAL CERVICAL MUSCULATURE IN AMNIOTA

The position

In Reptilia

Lower jaw: to it runs the musculus neuromandibularis in Serpentes (Nishi, 1938, p. 399).

Tongue bone: on it, especially on its corpus and caudal horn, attachment of the musculus episternohyoideus, sternohyoideus, cleidohyoideus, coracohyoideus, procoracohyoideus, omohyoideus a.s.o., occurring in different Reptilia (Nishi, 1938, p. 398).

In Aves

Tongue bone: attachment of several muscles, comparable to the musculus sternohyoideus (Nishi, 1938, p. 399).

Larynx: attachment of the musculus sternolaryngeus, a part of the deeper fascicles of the musculus sternohyoideus (Nishi, 1938, p. 399).

Trachea: attachment of the musculus sternotrachealis, a part of the deeper fascicles of the musculus sternohyoideus (Nishi, 1938, p. 399).

Syrinx: attachment of a number of special muscles, derived from the above mentioned muscles (Nishi, 1938, p. 399).

In Mammalia

Lower jaw: towards it may extend secondarily the musculus sternohyoideus (*Hystrix*, *Pteropus*) (Nishi, 1938, p. 416); to it may insert stray portions of the musculus omohyoideus (Nishi, 1938, p. 416).

Tongue bone: on the corpus and on its caudal horn normally insertion of the musculus sternohyoideus (NISHI, 1938, p. 416); on the tongue bone quite near to the attachment of the musculus sternohyoideus insertion of the musculus omohyoideus, which is lacking in a number of cases (certain Edentata, Rodentia, Insectivora, Chiroptera, Carnivora, Ungulata, Pinnipedia a.o.) (NISHI, 1938, p. 416).

Cartilago thyreoides: on it may insert stray portions of the musculus omohyoideus (*Tachyglossus*; *Homo*, var.) (NISHI, 1938, p. 416); on it ends the musculus sternothyreoideus (that is the caudal part of the musculus sternohyoideus profundus), which is seldom lacking (*Cavia*, *Balaenoptera*) (NISHI, 1938, p. 416); a linea or crista obliqua on the dorsal parts of the laminae of the cartilago thyreoides may indicate the place of insertion of the musculus sternohyoideus in Mammalia (GÖPPERT, 1937, p. 837).

16. PLACES OF ATTACHMENT OF THE DORSAL CERVICAL MUSCULATURE IN AMNIOTA

a. Introduction

Here may be repeated what has already been stated in § 11: that it is not possible when only "neck muscles" are mentioned, to ascertain whether we have here to deal with the dorsal cervical musculature, or with the dorsal trunk musculature situated in the neck.

b. The position

In Reptilia

Occipitale basilare: insertion of the musculus longus colli lateralis (NISHI, 1938, p. 400); insertion of the musculus longus colli ventralis *s.* basioccipitovertebralis (NISHI, 1938, p. 401).

In Mammalia

Occipitale basilare: sometimes origin of the musculus scalenus ventralis (NISHI, 1938, p. 417); insertion, sometimes partial, of the musculus longus capitis (NISHI, 1938, p. 418).

Sphenoideum: insertion, sometimes partial, of the musculus longus capitis (NISHI, 1938, p. 418).

Vomer: insertion, sometimes partial, of the musculus longus capitis (NISHI, 1938, p. 418).

17. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE HYOID ARCH IN PISCES

The position

Ethmoidal region: on the parethmoidal cartilage insertion of the musculus levator rostri in *Pristis* and Torpedinidae (LUTHER, 1938, p. 522).

18. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE BRANCHIAL ARCHES IN PISCES

a. The size of the place of attachment

Of Pisces in general GREGORY (1933, p. 437) mentions that in the upper half of the occiput above the exoccipitalia there are often deep fossae bordered by ridges for the insertion of the trapezius muscles of the shoulder-girdle. In *Tarpon atlanticus* (C. & V.) and some other Isospondyli these fossae are very deep (GREGORY, 1933, p. 437, fig. 32). In *Tarpon atlanticus* (C. & V.) the posttemporal fossae or fenestrae, through which the musculus trapezius passes, thus passing beneath the dermal skull roof, are large and the posterior end of the thin skull roof, which covers the space, in which this muscle lies, is lifted high above the level of the brain tube (GREGORY, 1933, pp. 139, 243).

b. The position

Skull (without detailed indication): partial origin of the musculus trapezius in *Polyodon* (LUTHER, 1938, p. 537).

Opisthoticum: origin of the musculus levator arcus branchialis V, which is homologous with the musculus trapezius in Squaliformes, in *Polypterus* (LUTHER, 1938, p. 537).

Pteroticum: origin of the musculus trapezius superficialis in Cyprinidae (LUBOSCH, 1938, p. 1019).

Processus postorbitalis: origin of the musculus trapezius in Holocephali (LUTHER, 1938, p. 533).

Epihyale and ceratohyale: attachment of the thick muscles that run to the cleithra in *Opsanus tau* (L.) (GREGORY, 1933, p. 383).

Pharyngobranchiale: dorsally on the osseous pharyngobranchiale III insertion of the musculus retractor arcuum branchialium dorsalis in *Amia* (LUTHER, 1938, p. 540).

Epibranchiale: on the epibranchiale VI, VII or VIII partial attachment of the last portion of the series of musculi constrictores 6, 7 or 8, in *Chlamydoselachus* and in other Squaliformes (LUTHER, 1938, pp. 526, 527); on the epibranchiale of the last branchial arch insertion of the rostral small fascicle of the musculus trapezius in Squaliformes, except in *Heterodontus japonicus* Dum. (LUTHER, 1938, p. 529).

Ceratobranchiale: on the ceratobranchiale VI, VII or VIII partial attachment of the last portion of the series of musculi constrictores 6, 7 or 8, in *Chlamydoselachus* and in other Squaliformes (LUTHER, 1938, pp. 526, 527); on ceratobranchiale IV and V attachment of the musculi pharyngo-claviculares in Teleostei, on the margin of ceratobranchiale V that of the musculi pharyngo-claviculares externi, on the top of ceratobranchiale V that of the interni (LUBOSCH, 1938, p. 1021).

19. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS FACIALIS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Quadratum: origin of the musculus quadratopectoralis in Salamandrinae and in *Amphiuma* (Lubosch, 1938, pp. 1043/1044).

Arcus branchialis: on arcus branchialis I attachment of the ventral fascicles of the musculus constrictor colli in the larval Salientia (Lubosch, 1938, p. 1046); this muscle is absent after metamorphosis in Salientia (Lubosch, 1938, p. 1045).

Ceratobranchiale: on the ceratobranchiale I origin of the accessory head or of caudal fascicles of the musculus constrictor colli in all adult Perennibranchiata (with the exception of *Amphiuma*) and in larval salamanders (Lubosch, 1938, pp. 1043, 1044); on the ceratobranchiale I entire origin of the musculus constrictor colli in larval Caudata, in later developmental stages partial origin on the ceratobranchiale I (Lubosch, 1938, p. 1044); this accessory head on the ceratobranchiale I disappears during metamorphosis of Caudata (Lubosch, 1938, pp. 1044/1045).

In Mammalia

Arcus zygomaticus: partial attachment of a mass of interwoven strands of muscles (inseparable sphincter with platysma) covering head and neck in Insectivora (Lubosch, 1938, pp. 1081/1082).

20. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS GLOSSOPHARYNGEUS AND THE NERVUS VAGUS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Cartilago lateralis: on it and its derivatives origin of all real larynx muscles in Amphibia (Göppert, 1937, p. 807); on the cartilago lateralis insertion of the musculus dilatator laryngis in Caudata (Göppert, 1937, p. 807); on the outer margin of the cartilago lateralis, of which only the top and the caudal end is left free, insertion of the musculus dorsopharyngeus in *Proteus* (Göppert, 1937, p. 807); on the outer side of the pars arytaenoidea of the cartilago lateralis in a long line insertion of the musculus dilatator laryngis in *Proteus* and *Necturus* (Göppert, 1937, p. 851).

Arytaenoid: attachment of the oral part of the musculus dorsopharyngeus which is more or less separated from the rest of this muscle and which can be called the musculus dorsolaryngeus, in Caudata; after metamorphosis this muscle is only left in Salamandridae (Göppert, 1937, pp. 807/808); on the broader part of the arytaenoid insertion of the musculus dorsolaryngeus in *Siren lacertina* L. (Göppert, 1937, p. 810); on the oral end of the narrower pars arytaenoidea of the cartilago lateralis insertion of the musculus dorsolaryngeus in *Amphiuma* (Göppert, 1937, p. 810); on the arytaenoid insertion of the musculus dilatator pharyngis in young larvae of Salientia, where it distinctly shows its origin from the musculus dorsopharyngeus (Göppert, 1937, p. 808); on the oral end of the narrow, rodlike arytaenoid insertion of the tendon of the musculus dilatator laryngis in larvae of Salamandridae (Göppert, 1937, p. 810); on a processus of the arytaenoid insertion of the end tendon of the musculus dilatator laryngis in larval *Ichthyophis glutinosus* L. (Göppert, 1937, p. 811); on the cartilago arytaenoidea insertion of the musculus dorsolaryngeus and on the larynx in general partial insertion of the musculus dorsopharyngeus in metamorphosed Amphibia (Lubosch, 1938, p. 1052).

Trachea: partial insertion of the musculus dorsopharyngeus in metamorphosed Amphibia (Lubosch, 1938, p. 1052).

21. PLACES OF ATTACHMENT OF THE MUSCULUS TRAPEZIUS AND ALLIED MUSCLES IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

a. The size of the places of attachment

The mastoid, to which the musculus sternocleidomastoideus is attached in Mammalia, only reaches the size of a processus mastoideus in *Homo*. This is connected with the erect walk and the development of the musculus sternocleidomastoideus (Stadtmüller, 1936, pp. 916, 991).

b. The position

In Amphibia

Skull (without detailed indication): origin of the musculus capiticlavicularis in Derotremata (*Cryptobranchus* (*Menopoma*)) and salamanders; this attachment on the skull develops during metamorphosis (Lubosch, 1938, p. 1059).

Occipitale: partial origin of the musculus capitiscapularis in Salientia (Lubosch, 1938, p. 1059).

Petrosum: partial origin of the musculus capitiscapularis in Salientia (Lubosch, 1938, p. 1059).

Tympanicum: partial origin of the musculus capitiscapularis in Salientia (Lubosch, 1938, p. 1059).

Lower jaw: on the inner surface of the supraangulare origin of the musculus interscapularis in Salientia (Lubosch, 1938, p. 1059).

In Reptilia

Occiput: on the occipitale laterale partial origin of the musculus capiticleido-episternalis in Sauria (Lubosch, 1938, p. 1061).

Processus paroticus: attachment of the musculus sternocleidomastoideus in Reptilia (Versluys, 1936, p. 741).

Temporal region: on the parietale and squamosum partial origin of the musculus capiti-cleido-episternalis in Sauria (Lubosch, 1938, p. 1061); on the squamosum origin of the musculus capitiplastralis in Testudinides (Lubosch, 1938, p. 1061).

In Aves

Occiput: on the squama occipitis partial origin of the musculus capiticlavicularis (Lubosch, 1938, p. 1061).

Processus postorbitalis: partial origin of the musculus capiticlavicularis (Lubosch, 1938, p. 1061).

Quadratum: partial origin of the musculus capiticlavicularis (Lubosch, 1938, p. 1061).

Lower jaw: on the articulare and angulare partial origin of the musculus capiticlavicularis (Lubosch, 1938, p. 1061).

In Mammalia

Occiput: attachment of the musculus cephaloclavicularis in part of the Mammalia (Lubosch, 1938, p. 1100); on the occipitale and the crista occipitalis partial origin of the musculus sternomastoideus (Lubosch, 1938, p. 1104); on the occipitale partial origin of the musculus cleidomastoideus, which is lacking in *Tachyglossus*, *Dasyurus* and *Manis* (Lubosch, 1938, p. 1104); on the basioccipitale partial origin of the superficial part of the musculus omocervicalis in *Tachyglossus* and in other Mammalia; this muscle is absent in *Bradypus*, *Myrmecophaga*, *Tatusia*, *Condylura*, *Talpa* and *Plecotus* (Lubosch, 1938, p. 1104).

Processus paroccipitalis: partial origin of the musculus sternomastoideus (Lubosch, 1938, p. 1104).

Regio otica: on the processus opercularis of the regio otica attachment of muscles of the shoulder-girdle in *Microtus* and *Sorex* (Stadtmüller, 1936, p. 874).

Pars mastoidea: partial origin of the musculus sternomastoideus (Stadtmüller, 1936, pp. 916, 991; Lubosch, 1938, p. 1104); partial attachment of the musculus sternomastoideus in *Bos* (Lubosch, 1938, p. 1103); entire attachment of the musculus sternomastoideus in *Sus* and *Canis* (Lubosch, 1938, p. 1103); entire or partial origin of the musculus cleidomastoideus in Mammalia, as f.i. in *Equus*, *Bos*, *Sus* and *Canis*; this muscle is lacking in *Tachyglossus*, *Dasyurus* and *Manis* (Lubosch, 1938, pp. 1103, 1104); partial origin of the superficial part of the musculus omocervicalis in *Tachyglossus* and other Mammalia; this muscle does not occur in *Bradypus*, *Myrmecophaga*, *Tatusia*, *Condylura*, *Talpa* and *Plecotus* (Lubosch, 1938, p. 1104).

Temporal region: origin of the musculus sternomastoideus in *Tachyglossus* (Lubosch, 1938, p. 1104); on the squamosum origin of the musculus sternomastoideus in *Ornithorhynchus*, *Dasyurus* and *Phalanger* (*Phalangista*) (Lubosch, 1938, p. 1104); on the squamosum origin of the musculus cleidomastoideus in *Ornithorhynchus* (Lubosch, 1938, p. 1104).

Lower jaw: as far as the lower jaw extension of the origin of the musculus sternomastoideus, the so-called musculus sternomassetericus (Lubosch, 1938, p. 1102); on it attachment of the musculus sternomandibularis in *Equus* (Lubosch, 1938, p. 1103).

22. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS HYPOGLOSSUS-CERVICALIS IN SAUROPSIDA AND IN MAMMALIA

The position

In Aves

Trachea: laterally attachment of the musculus sternotrachealis in Aves (Stresemann, 1937, p. 876); attachment of the musculus ypsilotrachealis in Anseres and *Chauna* (Stresemann, 1937, p. 878); insertion of two heads of the musculus sternotrachealis in the South American "Passeres tracheophonae", as f.i. in *Thamnophilus* (Stresemann, 1937, pp. 877/878); on the long upwardly directed process of the lowest tracheal ring, the so-called processus vocalis, and not on the trachea itself, attachment of the musculus sternotrachealis in *Furnarius* (Stresemann, 1937, p. 878).

23–31. PLACES OF ATTACHMENT OF MUSCLES RUNNING FROM THE SKULL TO SOFT PARTS OF THE HEAD

23. PLACES OF ATTACHMENT OF THE TONGUE MUSCULATURE

The position

In Pisces

Hyoid: on the cartilage of the hyoid origin of the musculus lissohyoglossus in *Polypterus*, the only genus among Pisces in which a tongue muscle occurs (Nishi, 1938, p. 447).

In Amphibia

Lower jaw: on the caudal angle of the chin origin of the musculus genioglossus in Salientia; this muscle does not occur in a number of genera, but does in others (Nishi, 1938, p. 448).

Tongue bone: on the processus thyreoideus of the tongue bone origin of the musculus hyoglossus in many genera of Salientia (Nishi, 1938, p. 448).

Copula: on the rostral top and on the dorsal side of the copula origin of the musculus hyoglossus in *Salamandra* which, together with the musculus basiradialis, constitutes a small muscle; this is partly attached to the caudal radius (Nishi, 1938, p. 448).

In Reptilia

Lower jaw: on the dentale origin of the musculus submentalis in *Gekko* and *Lialis*; this muscle is a separate portion of the musculus genioglossus (Nishi, 1938, p. 449).

Os entoglossum: origin of the musculus entoglossoglossus in *Trionyx* (Nishi, 1938, p. 450).

Cornu branchiale I: on its dorsal end origin of the musculus hyoglossus in *Chamaeleo* (Nishi, 1938, p. 449).

Larynx: attachment of the musculus geniolaryngeus in Serpentes (Nishi, 1938, p. 450).

Trachea: attachment of the caudal end of the musculus hyoglossus, the so-called musculus hyotrachealis in Serpentes (Nishi, 1938, p. 450); attachment of the musculus geniotrachealis in Serpentes (Nishi, 1938, p. 450).

In Mammalia

Basis cranii: partial origin of the musculus styloglossus in *Hylobates* (Nishi, 1938, p. 451).

Processus paramastoideus: partial origin of the musculus styloglossus in many Mammalia (Marsupialia, *Sciurus*, *Procavia*, *Tupaia*) (Nishi, 1938, p. 451).

Bulla auditiva: partial origin of the musculus styloglossus in *Chrotomys* (*Chrisotomys*) and Lemuroidae (Prosimiae) (Nishi, 1938, p. 451).

Tongue bone: on different parts of the tongue bone in Mammalia origin of the musculus hyoglossus which thus has been distinguished as musculus basioglossus, musculus chondroglossus and musculus ceratoglossus (Nishi, 1938, p. 451).

Stylohyale and processus styloides: entire or partial origin of the musculus styloglossus in Mammalia (Nishi, 1938, p. 451).

Cartilago thyreoides: origin of the musculus hyoglossus *s.* thyreoglossus in *Macaca* and *Cynocephalus* (Nishi, 1938, p. 451).

24. PLACES OF ATTACHMENT OF THE EYE MUSCULATURE

a. Introduction

In certain cases among Pisces part of the eye muscles are enclosed in a myodome or canalis muscularis or eye-muscle chamber. We have to distinguish a caudal and a rostral myodome. A rostral as well as a caudal myodome occurs in *Salmo* (Holmgren & Stensiö, 1936, pp. 484–487). In a few cases the myodome does not contain muscles, as *e.g.* in *Lepisosteus* (Holmgren & Stensiö, 1936, p. 472). In *Astroscopus y-graecum* (C. V.) there is no real myodome, but the eye muscles, portions of which are greatly hypertrophied and modified into electric organs, lie in the very large postorbital vacuities, as we shall discuss later on (Gregory, 1933, pp. 367/368, 439).

b. The size of the places of attachment

In stages of development

In Pisces

In embryonic and larval stages of typical Teleostei the myodome is a funnel-like tunnel (Gregory, 1933, p. 435).

In adult animals

In Pisces

The caudal myodome in †Cephalaspidae is in certain cases so large that the partition has partly disappeared (Holmgren & Stensiö, 1936, p. 254). In two carbonic and in one of the triassic †Palaeoniscidae the caudal myodome is small (Holmgren & Stensiö, 1936, pp. 399, 407). In †*Lepidotus* the caudal myodome is well developed (Holmgren & Stensiö, 1936, p. 480). In *Tarpon atlanticus* (C. & V.) the myodome is very capacious (Gregory, 1933, p. 140), in *Esox masquinongy* Mitchill it is not large (p. 216), whereas *Dactylagnus* shows the last traces of the myodome (p. 364). Holmgren & Stensiö (1936, p. 488) mention a number of Teleostei in which the myodome is very strongly reduced or even absent. The size and the differences in size may also be inferred from the position of the myodome in different Pisces which partly depends on the fact that the myodome consists of different parts which do not all occur in the different species of Pisces, so that the myodome in one species may be partly homologous with that in another species.

The rostral myodome in *Menidia* is small (Franz, 1934, p. 1046).

c. The position

In stages of development

In Pisces

In embryonic and larval stages of typical Teleostei, due to the very large eyes, the ventral eye muscles grow backward into the floor of the cranial vault (Gregory, 1933, p. 435). The anlage of the caudal myodome is also already present in young embryonic stages of *Amia* (Holmgren & Stensiö, 1936, p. 451). Young embryonic stages of *Salmo* show the anlage of the rostral myodome and of the caudal myodome, the latter containing the musculus rectus externus, part of the roof of this myodome being formed by the prootic bridge or dorsum sellae (Holmgren & Stensiö, 1936, pp. 484, 485).

In adult animals

The four musculi recti in Gnathostomata originate in the neighbourhood of the perforation in the wall of the orbita for the nervus opticus and thus originate on the caudal wall of the orbita. This general feature will not be mentioned for the different groups of the Gnathostomata separately. Only when this condition shows something remarkable, it will be mentioned in the following.

In Marsipobranchii

In Petromyzonidae five eye muscles originate from the bottom of the orbita, one from the caudal wall of the orbita; in Myxinoidea eye muscles are lacking (Nishi, 1938, p. 453).

In Pisces

As to the musculi recti we find, that in Holocephali the musculus rectus bulbi nasalis *s.* medius originates rostralward in the orbita (Nishi, 1938, p. 455); in Chondrostei the musculi recti originate from the nasal wall of the orbita; in *Neoceratodus* the four musculi recti originate deeply on the bottom of the orbita (Nishi, 1938, p. 456). In Holostei and in Teleostei the musculi recti also originate from the eye-muscle canal according to Nishi (1938, p. 455).

As to the caudal myodome we find the following remarks in literature.

In *Chlamydoselachus* part of the musculus rectus externus enters the orbital opening of the canalis transversus; this is perhaps an initial stage of a myodome according to Holmgren & Stensiö (1936, p. 317). According to Nishi (1938, pp. 454/455) it is the so-called musculus rectus temporalis accessorius that in *Chlamydoselachus* originates from the eye-muscle canal.

The caudal myodome in †Cephalaspidae lies behind the dorsum sellae in the ventral wall of the otical region and thus in the parachordal part of the basis cranii; right and left myodome are as a rule separated; they open at the postero-ventro-medial corner of each orbita (Holmgren & Stensiö, 1936, p. 254). The position of such an unpaired myodome in †Cephalaspidae can best be compared with that of †Palaeoniscidae, †*Saurichthys* and with the prootic part of that of *Amia* (Holmgren & Stensiö, 1936, p. 254).

In some carbonic †Palaeoniscidae we find an unpaired caudal myodome, which lies nearly entirely in the otical region (Holmgren & Stensiö, 1936, p. 399). It principally or slightly resembles that of the †Perleididae, †Ospiidae and †Belonorhynchidae

(†Saurichthyidae) (HOLMGREN & STENSIÖ, 1936, pp. 399, 417, 422). This myodome opens rostrally with one opening in each orbita (HOLMGREN & STENSIÖ, 1936, p. 399). In these fossils this myodome lies nearly completely in the rostral part of the floor of the otical region (HOLMGREN & STENSIÖ, 1936, p. 403).

In one of the triassic †Palaeoniscidae the myodome extends as for rostralward as the basisphenoid; not only the musculus rectus externus, but also the three other musculi recti had their origin in it; it is paired; this myodome constitutes the ventral half of a rather large hollow, the dorsal half being formed by the trigemino-facialis chamber (HOLMGREN & STENSIÖ, 1936, p. 407).

In *Amia* the caudal myodome lies partly beneath the dorsum sellae, the postclinoid wall of the myodome being formed by the prootic bridge; the caudal myodome is not separated from the trigemino-facialis chamber, the latter lying laterally and above, the caudal myodome lying more ventralwards and medially (HOLMGREN & STENSIÖ, 1936, pp. 456, 457).

In *Amia* and in †*Sinamia*, a fossil genus of Amiidae, the orbital parts of the myodome are separated from the trigemino-facialis chamber by a strong pedicle of the alisphenoid (HOLMGREN & STENSIÖ, 1936, p. 466). The musculus rectus externus in *Amia* originates from the walls of the caudal myodome, the three other musculi recti for the greater part from its opening (FRANZ, 1934, p. 1026).

In †*Lepidotus* the rostral part of the caudal myodome lies in the orbito-temporal region, for the greater part, however, it lies in the otic region; this myodome opens in the orbita with an opening which is bordered medially by the basisphenoid, laterally by the pedicle-like process of the prooticum (HOLMGREN & STENSIÖ, 1936, p. 480). In †*Hypsocormus* the caudal myodome is separated from the trigemino-facialis chamber by a cartilaginous or membranous part, which represents the alisphenoid-pedicle of *Amia* (HOLMGREN & STENSIÖ, 1936, p. 482).

In the adult *Salmo* the caudal myodome shows two parts. The ventral part contains parts of the musculi recti with the exception of the musculus rectus externus; this part is no doubt a caudal prolongation of the orbita (HOLMGREN & STENSIÖ, 1936, p. 487). The ventral part is separated from the dorsal part by a horizontal partition. The dorsal part of the myodome encloses the caudal part of the musculus rectus externus; it extends much more caudalward than the ventral part and extends even through the entire occipital region; generally it is considered as a partly extracranial, partly intracranial and intramural part (HOLMGREN & STENSIÖ, 1936, p. 487). This myodome in *Salmo* consists of three parts: the rostral part lies on the dorsal side of the trabeculae and polar cartilages and intracranially, the corpus basisphenoidei forms its roof; the middle part runs from the rostral margin of the prootic bridge caudalwards unto the beginning of the parachordalia, the prootic bridge forming its roof; it lies intramurally; the caudal part begins beneath the rostral margin of the parachordalia and lies extracranially; its most occipital part is bordered by a ventral lamella of the basioccipitale (HOLMGREN & STENSIÖ, 1936, pp. 487, 489, 490, 491; see also FRANZ, 1934, p. 1046).

A myodome, as *Salmo* shows, also occurs in a number of Teleostei; in some Teleostei the myodome represents only the dorsal part of that of *Salmo*, thus represents the myodome in *Amia* and encloses only the musculi recti externi; it lies entirely extracranially (HOLMGREN & STENSIÖ, 1936, pp. 488, 490; see also FRANZ, 1934, pp. 1046, 1058).

In *Tarpon atlanticus* (C. & V.) the myodome extends backward beneath the otic region, but does not open posteriorly (GREGORY, 1933, p. 140). In *Thunnus* we find an excavation of the basis cranii as part of the myodome (GREGORY, 1933, p. 311, fig. 191A).

As to the musculi obliqui the following was found. In Selachii the two musculi obliqui originate nasalward in the orbita (NISHI, 1938, p. 454). In *Neoceratodus* the two musculi obliqui originate side by side from the cranial wall of the orbita (NISHI, 1938, p. 456). In Holostei and in Teleostei the two musculi obliqui originate together from the so-called rostral eye-muscle canal in the rostral wall of the orbita (NISHI, 1938, p. 455).

A rostral myodome occurs in the adult *Salmo*. Here it lies in the ethmoidal cartilage and opens with a wide aperture in the orbita on both sides of the septum interorbitale; it has a median position and is unpaired; it is divided into two halves by a membranous septum which is the prolongation of the cartilaginous septum interorbitale, ending rostrally on the entrance of the rostral myodome (HOLMGREN & STENSIÖ, 1936, pp. 486, 487).

The shallow groove in the rostral wall of the orbita, in which the musculi obliqui in *Amia* originate, is called a rostral eye-muscle canal by FRANZ (1934, p. 1026). A rostral myodome for the musculi obliqui also occurs in *Menidia* (FRANZ, 1934, p. 1046).

In Amphibia

As to the musculi recti bulbi we find that in Apoda, if not entirely reduced, but still present, they do not originate on the skeletal wall of the orbita (Nishi, 1938, p. 457).

As to the musculi obliqui we mention the following. In Apoda they do not originate on the skeletal wall of the orbita either (Nishi, 1938, p. 457). In Caudata they originate quite closely to each other rostralward in the orbita (Nishi, 1938, p. 456); the same is the case in *Rana* (Nishi, 1938, p. 457).

As regards the musculus retractor bulbi the following facts may be mentioned. In Caudata it originates caudalward in the orbita on the parasphenoid (Nishi, 1938, p. 457). In *Rana* it originates together with the musculus rectus bulbi temporalis on the basisphenoid (Nishi, 1938, p. 457). In Apoda, where it acts as a musculus retractor tentaculi, it originates on the trabecular wall (Nishi, 1938, pp. 456, 458).

In Reptilia

The musculus retractor bulbi in *Sphenodon* originates in the caudal angle of the orbita on the base of the columella cranii (Nishi, 1938, p. 458). In Sauria the musculus retractor bulbi originates together with the musculus bursalis retractoris in the groove in the caudal angle of the orbita (Nishi, 1938, p. 458). These two muscles are lacking in *Chamaeleo* and in Serpentes (Nishi, 1938, p. 458).

The strongly developed musculus retractor palpebrae superioris in Loricata originates together with the musculus rectus bulbi temporalis from the orbita (Nishi, 1938, pp. 458, 459/460, 465).

In Aves

The two musculi obliqui originate together on the medial wall of the orbita (Nishi, 1938, p. 460). There is no musculus retractor bulbi in Aves (Nishi, 1938, p. 460).

In Mammalia

The musculus obliquus inferior maintains its original position. The origin of the musculus obliquus superior, however, is displaced caudalwards towards the depth of the orbita, next to the common origin of the musculi recti (Nishi, 1938, pp. 460, 461). In Monotremata the musculus obliquus superior does not originate so deeply in the bottom of the orbita as in higher Mammalia; in *Tachyglossus*, moreover, it is rostrally strengthened by fibres which originate from the frontale (Nishi, 1938, pp. 460/461).

d. Homology and non-homology

The differences in size and position of the myodomes are partly due to the fact that they are not homologous or only partly homologous.

The so-called myodome in *Chlamydoselachus* is probably not homologous with the caudal myodome in higher Pisces (Holmgren & Stensiö, 1936, p. 317). The myodome in one of the triassic †Palaeoniscidae represents only a rostral lateral part of the myodome of *Amia* and a small rostral lateral part of the dorsal portion of the myodome of Teleostei (Holmgren & Stensiö, 1936, p. 408); in some Teleostei the myodome represents only the dorsal part of the myodome in *Salmo* and represents the myodome in *Amia* (Holmgren & Stensiö, 1936, p. 488). The difference in opinion about the character of the myodome (Holmgren & Stensiö, 1936, pp. 487/488) is perhaps partly due to non-homology.

25. PLACES OF ATTACHMENT OF THE GENERAL VISCERAL MUSCULATURE IN MARSIPOBRANCHII

The position

In Myxinoidea

Places of attachment of muscles, innervated by the nervus trigeminus

Basal plate: on the ventral, lateral and partly also on the dorsal surface of the cartilaginous basal plate partial origin of the musculus tubulatus (Luther, 1938, p. 476).

Cartilago subnasalis: on its rostral end origin of the musculus subnasali-tentacularis (Luther, 1938, p. 473).

Chondroidal bar: on the so-called "inferior chondroidal bar" partial origin of the musculus tubulatus (Luther, 1938, p. 476).

Pharyngeal skeleton: on the rostral surface of the ventral part of the second arch of the pharyngeal skeleton, medialwards of the place of insertion of the musculus protractor cartilaginis basalis anterior, origin of the musculus retractor mucosae oris (Luther, 1938, p. 476).

Tentacular cartilage: on the ventral end of the support of the tentacular cartilage I and III, or closely in front of or behind it, insertion of the musculus trabeculo-coronarius (Luther, 1938, p. 474).

Velar cartilage: on its dorso-lateral surface insertion of the musculus spinovelaris (Luther, 1938, pp. 476/477).

In Petromyzonidae

α. Places of attachment of muscles, innervated by the nervus trigeminus

Cartilago trabecularis: partial attachment of the musculus basilaris (Luther, 1938, p. 480).

Cartilago rhomboidea: partial attachment of the musculus basilaris (Luther, 1938, p. 480).

Cartilago tectoria: partial attachment of the musculus basilaris (Luther, 1938, p. 480).

Cartilago apicalis: on its lateral wings attachment of the musculus apicalis lateralis (Luther, 1938, p. 480).

Cartilago glossa: insertion of the musculus basilariglossus, that is the outer part of the musculus mandibulariglossus, which is lacking in *Petromyzon marinus* L. (Luther, 1938, pp. 482/483).

Arcus subocularis: partial attachment of the musculus basilaris (Luther, 1938, p. 480).

β. Places of attachment of muscles, innervated by the nervus facialis, the nervus glossopharyngeus and the nervus vagus

Skull: ventralwards of the ear capsule partial origin of the musculus C_2e (musculus constrictor externus, N. VII) (Luther, 1938, p. 485).

Hypochordal longitudinal bar: origin of the musculus compressor branchiarum obliquus lateralis dorsalis (Luther, 1938, p. 488).

Ventral longitudinal bar: partial origin of the musculus compressor branchiarum obliquus lateralis ventralis (Luther, 1938, p. 488).

Branchial arches: on the surface of the most dorsal process of arcus branchialis I origin of some most caudal fibres of the musculus C_2e (musculus constrictor externus, N. VII) (Luther, 1938, p. 485); on the last branchial arch origin of fibres which adjoin the musculus constrictor internus caudalward and ventralward (Luther, 1938, p. 488).

26. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE MANDIBULAR ARCH IN PISCES

The position

Processus postorbitalis: origin of the musculus levator palpebrae nictitantis in *Sphyrna zygaena* Cuvier (Luther, 1938, p. 497).

Lower jaw: on the inner side of the mandibulare insertion of the ventral portion of the musculus spiracularis in a number of genera of Batoidei (*Trygon*, *Myliobatis*) (Luther, 1938, p. 495); this ventral portion is lacking in *Raja* (Luther, 1938, p. 495).

Hyomandibulare: partial or entire insertion of the musculus spiracularis in *Pristiophorus* and *Squatina* (Luther, 1938, pp. 495, 508); insertion of the dorsal or distal portion of the musculus spiracularis in typical Batoidei (Luther, 1938, pp. 495, 508).

27. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE HYOID ARCH IN PISCES

The position

Ethmoidal region: on the parethmoid partial insertion of the musculus depressor rostri in *Squatina* (LUTHER, 1938, p. 522).

Palatoquadratum: insertion of part of the rostral fibres of the dorsal part of the musculus constrictor 2 in many Squalidae (Spinacidae) (LUTHER, 1938, p. 518).

Lower jaw: on the mandibulare an extensive insertion of a strong superficial layer of the dorsal part of the musculus constrictor 2 in Hexanchidae (Notidanidae); this is connected with the fact that the hyoid arch is very slightly developed owing to the preponderance of the mandibular arch (LUTHER, 1938, pp. 518/519); on it insertion of one part of the ventral part of the musculus constrictor 2, the so-called musculus depressor mandibulae, in Batoidei (LUTHER, 1938, p. 522); on it insertion of one part of the musculus constrictor 2 in Lepidosireniformes (Dipneumones) (LUTHER, 1938, p. 525).

Hyomandibulare: attachment of part of the rostral fibres of the dorsal part of the musculus constrictor 2 in *Chlamydoselachus* (LUTHER, 1938, p. 517); on the dorsal side of the hyomandibulare insertion of the dorsal part of the musculus constrictor 2 in Carcharhinidae *Mustelus* and *Galeorhinus* (LUTHER, 1938, p. 519); on the hyomandibulare insertion of the rostral part of the dorsal part of the musculus constrictor 2 in *Squatina* (LUTHER, 1938, p. 522); insertion of one part of the ventral part of the musculus constrictor 2, the so-called musculus depressor hyomandibularis in Batoidei (LUTHER, 1938, p. 522).

Hyoid: origin of fibres of the ventral part of the musculus constrictor 2 in *Chlamydoselachus* (LUTHER, 1938, p. 517); on the "hyale" partial insertion of a small fascicle of the dorsal part of the musculus constrictor 2 in Hexanchidae (Notidanidae); this is connected with the fact that the hyoid arch is very slightly developed owing to the preponderance of the mandibular arch (LUTHER, 1938, p. 518).

Operculum: partial insertion of the musculus opercularis in ganoids (LUTHER, 1938, p. 524).

28. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE BRANCHIAL ARCHES IN PISCES

a. The size of the place of attachment

A correlation seems to exist between the development of the extrabranchialia in Squaliformes and that of the musculi constrictores in as much as there is a connection between the development of these cartilages and the size of the gill slits and the degree in which these musculi constrictores overlap each other (LUTHER, 1938, p. 527). There is also a correlation between the development of the musculi constrictores in Batoidei and the position of the gill slits and the far rostral position of the pinnae pectorales (LUTHER, 1938, p. 531). There is also a correlation between the reduction of the musculi constrictores in Holocephali and the reduction of the interbranchial septa (LUTHER, 1938, p. 532).

b. The position

Branchial arches (without detailed indication): attachment of the fibres of the musculus sphincter oesophagi in Chondrostei, not in *Polypterus* (LUTHER, 1938, p. 539).

Epibranchiale: on the epibranchialia insertion of the inner (proximal) dorsal fibres of the musculi constrictores in *Chlamydoselachus* (LUTHER, 1938, p. 526); on the mediocaudal margin of the epibranchiale I partial origin of the musculus interbranchialis in *Acipenser ruthenus* L. (LUTHER, 1938, p. 535); on epibranchiale IV attachment of the musculus obliquus dorsalis medialis of arcus V (LUBOSCH, 1938, p. 1018).

Ceratobranchiale: on the ceratobranchialia attachment of the inner (rostral) ventral fibres, in the same way as the dorsal fibres are inserted on the epibranchiale, in *Chlamydoselachus* (LUTHER, 1938, p. 526); on the mediocaudal margin of ceratobranchiale I partial origin of the musculus interbranchialis in *Acipenser ruthenus* L. (LUTHER, 1938, p. 535).

Extrabranchialia: on their outer side origin of the musculi constrictores in pentanch sharks (LUTHER, 1938, p. 527).

Operculum: on its inner side dorsal of the gill opening the greater part of the origin of the musculus interbranchialis which lies in the caudal wall of the 4th gill pouch in Holocephali (LUTHER, 1938, pp. 532/533).

29. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS TRIGEMINUS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Lateral side of the skull: on parietale, prooticum, frontale, praefrontale, nasal capsule the greater part of the attachment of the musculus levator bulbi in Caudata and Salientia (LUBOSCH, 1938, pp. 1025, 1026).

Lower jaw: on the Meckelian cartilage attachment of the musculus mandibulolabialis in Amphibia (LUBOSCH, 1938, p. 1038).

In Reptilia

Lateral side of the skull: on the wall of the cerebral capsule and on the parietale origin of the musculus levator bulbi dorsalis in Sauria (LUBOSCH, 1938, p. 1028).

In Mammalia

Bulla tympani: on the tympanicum partial attachment of the musculus tensor veli palatini in adult Mammalia (LUBOSCH, 1938, p. 1072); on the bulla tympani partial origin of the musculus tensor veli palatini in Rodentia and Lemuroidae (Prosimiae); origin of the musculus tensor veli palatini in Chiroptera and *Dasypus* (Lubosch, 1938, p. 1073); on the tympanicum origin of the musculus tensor veli palatini in *Elephas* (Lubosch, 1938, pp. 1073/1074).

Cartilage of the tuba auditiva: origin of the musculus tensor veli palatini in Carnivora; partial origin of the musculus tensor veli palatini in Rodentia and Lemuroidae (Prosimiae) (Lubosch, 1938, p. 1073).

30. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS FACIALIS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

a. The size of the place of attachment

In Mammalia

The enormous development of the proboscis in Proboscidea with their strong muscles (musculus maxillo-labialis and parts of the musculus buccinatorius) result in a large size of the place of attachment of these muscles on the upper jaw and partly also on the frontale. This large place of attachment is possible as it lies at some distance from the cerebral capsule, nasal capsule, the space between them being filled by spongious or pneumatic bone (Weber, 1927 I, p. 53).

b. The position

In Mammalia

Basis cranii: partial origin of the musculus maxillolabialis in *Talpa* (Lubosch, 1938, p. 1090).

Dorsal surface of the skull: origin of the musculus temporobuccalis in *Erinaceus* (Lubosch, 1938, p. 1082); on the roof of the skull origin of the musculus auricularis posterior, musculus auricularis superior and musculus auricularis inferior in Mammalia (Lubosch, 1938, p. 1085).

Occipitale: partial origin of the platysma of the neck in Mammalia (Lubosch, 1938, p. 1083); attachment of the musculus auriculo-occipitalis in Mammalia (Lubosch, 1938, p. 1083); on the occiput origin of the musculus auricularis posterior, musculus auricularis superior and musculus auricularis inferior in Mammalia (Lubosch, 1938, p. 1085).

Meatus auditorius externus: on this osseous and cartilaginous meatus attachment of the musculus auriculo-mandibularis in all Mammalia, except the Primates (Lubosch, 1938, pp. 1084/1085); on the osseous meatus auditorius externus partial origin of the musculus maxillolabialis in *Talpa* (Lubosch, 1938, p. 1090).

Arcus zygomaticus: attachment of the preauricular group of the platysma, the so-called portio zygomatico-auricularis in *Erinaceus* (Lubosch, 1938, p. 1082); attachment of the musculus auriculo-mandibularis in all Mammalia, except the Primates (Lubosch, 1938, pp. 1084/1085); attachment of the musculus zygomatico-labialis in *Erinaceus* (LUBOSCH, 1938, p. 1088); attachment of the musculus sternofacialis in Rodentia and *Procavia* (LUBOSCH, 1938, p. 1089).

Forehead: attachment of the musculus occipito-frontalis *s.* musculus orbito-fronto-auricularis in Mammalia (LUBOSCH, 1938, p. 1085); on the frontale or on the bridge of the nose attachment of the musculus nasolabialis in Mammalia (LUBOSCH, 1938, p. 1088).

Margin of the orbita: on the margo supraorbitalis partial attachment of the deeper fibres of the musculus auriculo-occipitalis in some Marsupialia (*Myrmecobius*) (LUBOSCH, 1938, p. 1083); on the margin of the orbita attachment of the musculus orbicularis oculi in Mammalia with an extension on the processus frontalis maxillae and the bridge of the nose in Pongidae and *Homo* (LUBOSCH, 1938, p. 1088).

Upper jaw: attachment of the musculus orbicularis oris in Monotremata (LUBOSCH, 1938, p. 1080); on the maxillare origin of the platysma in *Tachyglossus* and *Ornithorhynchus* (LUBOSCH, 1938, p. 1081); on the upper jaw origin of the musculus maxillolabialis or musculus levator labii superioris proprius or the caput infraorbitale musculi quadrati labii superioris of *Homo* (LUBOSCH, 1938, p. 1090).

Jaw joint: attachment of the musculus auriculo-mandibularis in all Mammalia, except the Primates (LUBOSCH, 1938, pp. 1084/1085).

Lower jaw: attachment of the musculus quadratus labii inferioris in Primates (LUBOSCH, 1938, p. 1083); on its ventral surface origin of the musculus transversus menti in *Myocastor* (*Myopotamus*), *Lepus* and *Dolichotis* (LUBOSCH, 1938, p. 1090); on the processus coronoideus origin of the musculus buccolabialis in *Neomys* (*Crossopus*) (LUBOSCH, 1938, p. 1090); insertion of the musculus masto-mandibularis *s.* jugulomandibularis in *Equus caballus* L. (LUBOSCH, 1938, p. 1093).

31. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS GLOSSOPHARYNGEUS AND THE NERVUS VAGUS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Branchial arches: on a tendinous plate surrounding the top of the arcus branchialis IV attachment of the musculus levator arcus in adult *Siphonops* (LUBOSCH, 1938, p. 1054); on the arcus branchialis IV insertion of the musculus vertebro-hyoideus in *Hypogeophis*, where this muscle has the same position as the musculus levator in adult *Siphonops* (LUBOSCH, 1938, p. 1054); on the ceratobranchialia II, III and IV origin of the musculi levatores branchiarum; on the ceratobranchialia I, II and III origin of the musculi depressores branchiarum in *Siredon* and larvae of *Salamandra* and of *Triturus* (LUBOSCH, 1938, p. 1054).

Larynx: on the cricoid attachment of the musculus cricolabialis in Salientia (GÖPPERT, 1937, p. 809).

Trachea: partial attachment of the diaphragm-like part of the musculus dorsopharyngeus in Apoda (LUBOSCH, 1938, p. 1055).

In Mammalia

Petrosum and bulla auditiva: entire origin of the musculus palato-pharyngeus in Artiodactyla and partial origin in other Mammalia; in yet other Mammalia origin entirely (Marsupialia, Rodentia, *Equus*) or partly on the wall of the tuba auditiva; in Monotremata, *Delphinus* and *Elephas* this muscle is lacking (Lubosch, 1938, p. 1098).

Pterygoideum: on the hamulus of the pterygoid the most constant and as a rule the only origin of the musculus cephalopharyngicus in Mammalia; this origin is lacking in Monotremata, *Myrmecophaga* and *Orycteropus* (Lubosch, 1938, p. 1097); on the hamulus of the pterygoid origin of the musculus pterygo-pharyngeus (Lubosch, 1938, p. 1097).

Lower jaw: partial origin of the musculus cephalopharyngicus in Primates (Lubosch, 1938, p. 1097).

Tongue bone: on the cornu hyale and the cornu thyreale origin of the musculus constrictor pharyngeus medius (Lubosch, 1938, p. 1097).

Hyoid arch: origin of the musculus hyobuccalis in *Myrmecophaga* (Lubosch, 1938, p. 1096).

Larynx: as a rule partial origin of the musculus constrictor pharyngeus medius in Mammalia (Lubosch, 1938, p. 1097); attachment of the longitudinal part of the musculus pharyngopalatinus, the so-called musculus palatothyreoideus; this longitudinal part is lacking in *Elephas* (Lubosch, 1938, p. 1098).

32–39. PLACES OF ATTACHMENT OF MUSCLES CONNECTING CORRESPONDING SKULL ELEMENTS OF THE RIGHT AND LEFT SIDE

This is a compilation of remarks in literature on the places of attachment of muscles connecting skull elements of the right and of the left side. These muscles may run straight, but they may also curve round an element of the skull or head as *e.g.* the larynx or the pharynx. One muscle may connect the two skull elements, there may be a more or less continuous connection between the right and the left muscle, the muscle being unpaired or paired, and there may be a narrow or broad connection of connective tissue in the median plane between the two antimeres.

32. PLACES OF ATTACHMENT OF THE TONGUE MUSCULATURE

The position

In Amphibia

Tongue bone: on the top of the radius of the tongue bone attachment of the musculus interradialis in *Triturus*, which stretches between the tops of these radii of right and left side (Nishi, 1938, p. 448).

33. PLACES OF ATTACHMENT OF THE GENERAL VISCERAL MUSCULATURE IN MARSIPOBRANCHII

The position

In Petromyzonidae

Places of attachment of muscles, innervated by the nervus trigeminus

Trabecular plate: partial attachment of the ring-like musculus pharyngeus by some strands of connective tissue (LUTHER, 1938, p. 481).

Cartilago rhomboidea: on the inner surface of its middle part partial attachment of the ring-like musculus pharyngeus (LUTHER, 1938, p. 481).

Cartilago tectoria: rostrally on its caudal margin partial attachment of the ring-like musculus pharyngeus (LUTHER, 1938, p. 481).

Mandibular arch: on both sides of the pars styloidea of the mandibular arch partial origin of the arch-like musculus pharyngeus posterior (LUTHER, 1938, p. 484).

Mandibulare: on the right and on the left side origin of fibres of the ring-like musculus mandibularis posterior (LUTHER, 1938, p. 482).

34. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE MANDIBULAR ARCH IN PISCES

The position

Lower jaw: on its two halves, connecting them both ventrally, attachment of the musculus constrictor 1 ventralis *s.* intermandibularis in Selachii (LUTHER, 1938, pp. 494, 502); this muscle seems to be lacking entirely in *Chlamydoselachus* (LUTHER, 1938, p. 503); near the symphysis attachment of some fibres of the musculus intermandibularis anterior, caudalwards on the mandibula attachment of the rest of the musculus intermandibularis anterior in true Batoidei, in which this muscle is not seldom partly or entirely lacking (LUTHER, 1938, p. 503); partial attachment of the musculus intermandibularis posterior in *Rhinobatus*, entire attachment in *Raja* and *Trygon*, while in *Myliobatis* this muscle has been lost (LUTHER, 1938, p. 503); on its external surface attachment of the musculus intermandibularis posterior profundus in *Narke* (*Astrape*) (LUTHER, 1938, p. 503); on the abdental margin of the mandibulare and of the dentale origin of that part of the musculus constrictor 1 + 2 ventralis called the musculus intermandibularis in *Polyodon* (LUTHER, 1938, p. 510); on the mandibulare origin of the musculus intermandibularis in Acipenseridae (LUTHER, 1938, p. 510); on the cartilage of MECKEL and on the spleniale origin of the musculus intermandibularis in Crossopterygii (LUTHER, 1938, p. 512); on the lower jaw from the symphysis to the jaw joint origin of the musculus intermandibularis in *Lepisosteus* (LUTHER, 1938, p. 515); on the left and right dentale origin of the musculus constrictor 1 ventralis *s.* intermandibularis anterior in Teleostei (LUBOSCH, 1938, p. 1014).

Hyale: on its outer half attachment of the musculus constrictor 1 + 2 ventralis profundus in Chondrostei (LUTHER, 1938, p. 510); ventrally on the ceratohyale origin of the more caudal part of the musculus constrictor 1 + 2 ventralis, the so-called musculus hyohyoideus, in *Polyodon* (LUTHER, 1938, p. 510).

Operculum: on it, partly medially on the interoperculum, origin of the most caudal part of the musculus constrictor 1 + 2 ventralis in *Polyodon* (LUTHER, 1938, p. 510).

35. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE HYOID ARCH IN PISCES

The position

Lower jaw: on the mandibulare almost as far as the symphysis origin of ventral fibres of the musculus constrictor 2 in *Chlamydoselachus* which constitute a superficial layer, the so-called musculus intermandibularis (LUTHER, 1938, p. 518); in most other genera of Squaliformes there is – different from *Chlamydoselachus* – superficially no distinct demarcation between the portion of the ventral part of the musculus constrictor 2 which is attached to the mandibulare and the portion of the ventral part of the musculus constrictor 2 which is attached to the hyoid arch (LUTHER, 1938, p. 520); on the ventral margin of the mandibulare partial origin of the ventral portion of the musculus constrictor 1 + 2, the so-called musculus intermandibularis, in Lamnidae and in Carcharhinidae (LUTHER, 1938, p. 521); on the abdental margin of the mandibula insertion of the rostral fibres of the musculus hyoideus inferior of the opposite side in Holocephali (LUTHER, 1938, p. 523); on the Meckelian cartilage attachment of the musculus intermandibularis in *Polypterus* and *Calamoichthys* (LUTHER, 1938, p. 524).

Hyale: on its caudal half or its caudal three quarters origin of the deep layer of the ventral part of the musculus constrictor 2 in Squaliformes (LUTHER, 1938, p. 521); origin of the musculus hyoideus inferior in Holocephali (LUTHER, 1938, p. 523); origin of the rostral part of the musculus constrictor 2, the so-called musculus protractor hyoidei *s.* musculus interhyoideus, in Lepidosireniformes (Dipneumones) (LUTHER, 1938, p. 525); on the ceratohyale partial insertion of the musculus protractor hyoidei (part of the ventral portion of the musculus constrictor 2) in *Polypterus* and *Calamoichthys* (LUTHER, 1938, p. 524).

Operculum: on its ventral part partial insertion of the musculus protractor hyoidei (part of the ventral portion of the musculus constrictor 2) in *Polypterus* and *Calamoichthys* (LUTHER, 1938, p. 524).

36. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE BRANCHIAL ARCHES IN PISCES

The position

Basis cranii: lateral of the median plane partial attachment of the musculus constrictor pharyngis in *Protopterus* and *Lepidosiren*; the continuation of this muscle oralward is the musculus interbranchialis of the last branchial arch (GÖPPERT, 1937, p. 798).

Branchial arches (without detailed indication): between the two sides of the last branchial arches run the musculi interarcuales *s.* interbranchiales in Pisces (Göppert, 1937, p. 809); on the branchial arches attachment of the musculus transversus ventralis in ganoids (Luther, 1938, p. 537); on the caudal margin of the last branchial arch partial origin of the musculus constrictor oesophagi in Selachii (Luther, 1938, p. 539); on the ventral part of the last branchial arch partial insertion of the most rostral fibres of the musculus constrictor oesophagi in *Squalus acanthias* L. (Luther, 1938, p. 539); on the branchial arch V partial attachment of the musculus transversus dorsalis in *Acipenser ruthenus* L. (Luther, 1938, p. 540).

Pharyngobranchiale: on the pharyngobranchiale III attachment of the musculus transversus in *Amia* (Luther, 1938, p. 540); on the caudal pharyngobranchiale attachment of the musculus transversus dorsalis posterior in some Teleostei (Lubosch, 1938, p. 1019).

Ossa pharyngea superiora: attachment of fascicles of the musculus constrictor pharyngis in *Leuciscus* (Lubosch, 1938, p. 1022).

Epibranchiale: on the left and right epibranchiale II insertion of the musculus transversus dorsalis anterior, connecting these two epibranchialia, in some Teleostei (Lubosch, 1938, p. 1019); on the epibranchiale IV attachment of the musculus transversus dorsalis in *Polyodon* (Luther, 1938, pp. 539/540); on the epibranchiale IV partial attachment of the musculus transversus dorsalis in *Acipenser ruthenus* L. (Luther, 1938, p. 540); on the epibranchiale IV attachment of the musculus transversus dorsalis posterior in some Teleostei (Lubosch, 1938, p. 1019).

Ceratobranchiale: on the ceratobranchiale IV partial attachment of the musculus transversus dorsalis in *Acipenser ruthenus* L. (Luther, 1938, p. 540); on the ceratobranchiale V attachment of the musculus constrictor pharyngis in *Leuciscus* (Lubosch, 1938, p. 1022).

Cardiobranchiale: ventrally on its caudal process the main insertion of the musculus constrictor oesophagi in *Squalus acanthias* L. (Luther, 1938, p. 539).

Os pharyngeale inferius: an intermediary attachment of the fascicles of the musculus constrictor pharyngis in *Leuciscus* (Lubosch, 1938, p. 1022).

37. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS TRIGEMINUS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Lower jaw: on its ventral surface near the symphysis the paired origin of the musculus intermandibularis anterior in larval stages of Caudata in adult Derotremata and in all Salientia (Lubosch, 1938, p. 1038); on the ventral end of the Meckelian cartilage origin of the musculus intermandibularis anterior in larval stages of Salientia and on the lateral surface of the dentale in adult Salientia (Lubosch, 1938, p. 1038); on the dentale and goniale as far as in the region of the processus coronoideus origin of the musculus intermandibularis posterior in Amphibia, as far as the spleniale in *Siredon* and *Necturus* (*Menobranchus*) (Lubosch, 1938, p. 1038); on the Meckelian cartilage origin of the musculus intermandibularis posterior in larval stages of Salientia (Lubosch, 1938, p. 1039).

In Reptilia

Lower jaw: origin of the musculus intermandibularis posterior ventralis in Serpentes, on its medial surface origin of the musculus intermandibularis posterior dorsalis in Serpentes and on the lateral surfaces of its rostral ends origin of the musculus intermandibularis anterior in Serpentes (Lubosch, 1938, p. 1041).

In Mammalia

Lower jaw: on its inner surface attachment of the musculus intermandibularis superficialis in *Tachyglossus*, where it is a proper intermandibular muscle (Lubosch, 1938, p. 1077).

38. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS FACIALIS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Quadratum: partial origin of the musculus interhyoideus in *Siren*, *Cryptobranchus* (*Menopoma*) and larval *Siredon* (Lubosch, 1938, p. 1044).

Lower jaw: on its process – and not on the arcus hyalis – origin of the musculus interhyoideus in Apoda (Lubosch, 1938, p. 1045); on it origin of the musculus interhyoideus in *Pipa* (Lubosch, 1938, p. 1046).

Tongue bone: on its cornu principale origin of the musculus interhyoideus, the so-called musculus subhyoideus, in adult *Rana* (Lubosch, 1938, p. 1045).

Hyale: on its processus laterales attachment of the musculus interhyoideus (anterior) in larval Salientia (Lubosch, 1938, p. 1047); on the ceratohyale origin or partial origin of the musculus interhyoideus in Perennibranchiata (Lubosch, 1938, p. 1044); on the ceratohyale origin of the musculus interhyoideus in larval Caudata, which muscle is not divided into two portions until metamorphosis (Lubosch, 1938, p. 1045).

In Reptilia

Tongue bone: attachment of the musculus interhyoideus in embryonic *Lacerta*, in *Sphenodon*, *Gekko* and *Chelonia* (Lubosch, 1938, pp. 1047, 1049).

In Mammalia

Hyoid arch: on its dorsal margin attachment of the musculus interhyoideus primitivus in Mammalia (Lubosch, 1938, p. 1091).

39. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS GLOSSOPHARYNGEUS AND THE NERVUS VAGUS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Petrosum: attachment of the first musculus petrohyoideus which is connected with its antimere ventrally of the larynx in *Kalomella*, *Microhyla* (*Mikrohyale*) and *Cacosternum* (Lubosch, 1938, p. 1057); attachment of the musculus petrohyoideus posterior III which is connected with its antimere dorsally of the larynx in some Microhylidae (Brevicipitidae) (Lubosch, 1938, p. 1057); in Pipidae (Aglossa) only one musculus petrohyoideus is present (Lubosch, 1938, p. 1057); attachment of the oral fibres of the musculus petrohyoideus which run without interruption from one side to the other in the adult *Pipa pipa* L. (*Pipa americana*) (Lubosch, 1938, p. 1057).

Tongue bone: on the end of the osseous part of its processus posteromedialis origin of the musculus hyolaryngeus in some Salientia, as *e.g. Rana*, after metamorphosis (Göppert, 1937, p. 811); on the basal part of its processus posteromedialis origin of the musculus sphincter of the larynx in most adult species of Salientia (Göppert, 1937, p. 811).

Branchial arches (without detailed indication): attachment of the musculi transversi ventrales, connecting the branchial arches of the left and right side, in Caudata and in Apoda (Lubosch, 1938, p. 1051); on the most caudal branchial arch attachment of the musculus hyopharyngeus which is obviously the original condition among Amphibia; this place of attachment is lost with the reduction and reconstruction of this arch to the cartilago lateralis (Göppert, 1937, p. 807); on the most caudal branchial arches attachment of the musculus hyopharyngeus, extending between those of the right side and the left, in Salamandrinae; when during metamorphosis arcus branchialis IV in Caudata disappears, the lateral end of the musculus hyopharyngeus attaches itself to the musculus levator arcus branchialis IV (Göppert, 1937, p. 806); on the arcus branchialis IV, which later on fuses with no III, origin of the musculus dorsopharyngeus with the exception of its most caudal part, in larval *Ichthyophis* (Göppert, 1937, p. 808); on arcus branchialis IV partial origin of the musculus diaphragmatico-branchialis lateralis in larval Salientia, this muscle can be compared with a musculus hyopharyngeus, it atrophies during metamorphosis (Lubosch, 1938, pp. 1055, 1056).

Epibranchiale: on the dorsal end of the epibranchiale III attachment of a musculus transversus ventralis in the adult *Siphonops*, this muscle meets that of the other side ventrally of the trachea (Lubosch, 1938, p. 1054).

Ceratobranchiale: on the ceratobranchialia attachment of the musculi interarcuales ventrales obliqui, which run to the median plane, in Caudata and larval Salientia (Lubosch, 1938, pp. 1051/1052); to the ventral ends of the ceratobranchialia II and III origin of the two musculi interarcuales ventrales obliqui in Caudata; these muscles disappear during metamorphosis (Lubosch, 1938, p. 1053); on the dorsal segment of the arcus branchialis

III origin of the main part of the musculus hyopharyngeus in *Necturus* and *Proteus*, in which the arcus branchialis IV is lacking (Göppert, 1937, p. 807); on the ceratobranchiale II attachment of a rostral part of the musculus hyopharyngeus in *Necturus* (*Menobranchus*) and in *Siren* (Lubosch, 1938, p. 1052).

Arytaenoid: on the marginal parts of the pars arytaenoidea of the cartilago lateralis entire origin of the musculi laryngei dorsales and ventrales in *Proteus* and partial origin of the same muscles in *Necturus* (Göppert, 1937, p. 809); on the dorsal and ventral surfaces of the broader part of the pars arytaenoidea of the cartilago lateralis partial origin of the musculi laryngei in *Siren lacertina* L. (Göppert, 1937, p. 810); on a processus of the arytaenoid insertion of remains of the musculus laryngeus ventralis in larval *Ichthyophis glutinosus* (L.) (Göppert, 1937, p. 811).

In Reptilia

Corpus hyoidei: ventrally partial origin of the musculus sphincter laryngis in Sauria (Göppert, 1937, p. 821); ventrally origin of the musculus sphincter laryngis in Testudinides (Göppert, 1937, p. 821).

Arytaenoid: caudally on the broad arytaenoid origin of the musculus laryngeus dorsalis in *Natrix* (*Tropidonotus*); most fibres of the right and left muscle meet dorsally in a median raphe (Göppert, 1937, pp. 820/821).

Cricoid: on its processus cranialis medianus ventralis partial origin of the musculus sphincter laryngis in Sauria (Göppert, 1937, p. 821); ventrally on the cricoid partial origin of the musculus sphincter laryngis in Loricata (Göppert, 1937, p. 821).

In Aves

Arytaenoid: on the margin of its dorsal surface attachment of the dorsal part of the muscles which can close the larynx, the so-called musculus interarytaenoideus, the muscles of the right and left side meeting each other in a dorsal raphe in Aves (Göppert, 1937, p. 829); on its dorsal surface, along the border of the lateral incision origin of the musculus interarytaenoideus, which meet each other in a medial raphe, in *Struthio camelus* L. (Göppert, 1937, p. 829).

Cricoid: on its margin, more caudalwards on the outer side and finally on its dorsal surface, partial origin of the muscles which can close the larynx, the caudal parts of which enclose the larynx; the muscles from the right and left side meeting each other in a raphe, thus forming a paired musculus sphincter in Aves (Göppert, 1937, pp. 828/829); on the cricoid origin of the musculus sphincter, adjoining the origin of the musculus crico-arytaenoideus lateralis towards the side of the trachea; the musculus sphincter from the right and left side meet each other in a median raphe in *Struthio camelus* L. (Göppert, 1937, p. 829).

In Mammalia

Palatinum: on its caudal margin partial origin of lateral fibres of the musculus pharyngopalatinus in Mammalia (Lubosch, 1938, p. 1097).

Stylohyale: origin of the musculus stylopharyngicus, which is entirely or partly (*Erinaceus*, Carnivora, *Equus*) a sphincter (Lubosch, 1938, p. 1096).

Cartilago thyreoides: partial origin of the musculus sphincter pharyngolaryngeus, especially of the so-called pars thyreoidea, in Mammalia (Lubosch, 1938, p. 1096); partial origin of a superficial layer of the musculus thyreo-arytaenoideus which meets the antimere in the medial plane, in *Equus caballus* L. and *Canis familiaris* L.; the same is the case with a separate fascicle of this muscle in *Alopex lagopus* (Merriam) (*Canis lagopus*) (Göppert, 1937, p. 853); on the edges of its incisura mediana inferior attachment of the musculus thyreoideus transversus in *Ursus*, *Procyon* and *Hylobates* (Göppert, 1937, p. 855).

Arytaenoid: attachment of the musculus interarytaenoideus *s.* arytaenoideus transversus, running between the right and the left arytaenoid, in those Marsupialia and Eutheria (Placentalia), as *e.g.* the Primates, in which the proarytaenoid is either lacking or very small or in which for another reason rostral fibres of the two antimeres meet each other in a median raphe (Göppert, 1937, pp. 852, 854); partial insertion of a superficial layer of the musculus thyreo-arytaenoideus which meets the antimere in the medial plane in *Equus caballus* L. and *Canis familiaris* L.; the same is the case with a separate fascicle of this muscle in *Alopex lagopus* (Merriam) (*Canis lagopus*) (Göppert, 1937, p. 853).

Cartilago cricoidea: partial attachment of the musculus sphincter pharyngolaryngeus, especially of the so-called pars cricoidea in Mammalia (Lubosch, 1938, p. 1096); attachment of the musculus retractor oesophagi in *Tachyglossus* (Lubosch, 1938, p. 1097).

Trachea: partial origin of the musculus sphincter pharyngolaryngeus in *Orycteropus* and as variations in *Nycticebus* (*Stenops*), *Pan* and *Homo* (Lubosch, 1938, p. 1096).

40–51. PLACES OF ATTACHMENT OF MUSCLES RUNNING BETWEEN DIFFERENT PARTS OF THE SKULL

The muscles belonging to this group may be expected to teach us all kinds of things about the influence of the character of the attachment *e.g.* a large surface or a small one on the relief of the cranial surface, because they may differ in the origin of a muscle and in its insertion.

40. PLACES OF ATTACHMENT OF THE EPIBRANCHIAL MUSCULATURE IN PISCES

The position

Ventral surface of the caudal part of the skull: partial origin of the musculus subspinalis *s.* musculus protractor arcuum branchialium in Squaliformes and in Holocephali (Nishi, 1938, p. 368).

Branchial arches: on the pharyngobranchialia I, respectively I and II, insertion of the musculus subspinalis in certain cases among Squaliformes (Nishi, 1938, p. 368); a small dorsal part of the muscle only is inserted on the pharyngobranchiale I in Hexanchidae (Notidanidae) and in most pentanch sharks, on the pharyngobranchialia I and II in *Mustelus* and in

Holocephali (Nishi, 1938, p. 368); the pharyngobranchialia of the consecutive branchial arches are connected by the short musculi interbasales *s.* interpharyngobranchiales *s.* interarcuales; their number in Squaliformes is five, four, three, two or none, in Holocephali only one; these musculi interbasales are lacking in Batoidei and in the other higher Pisces (Nishi, 1938, p. 368).

41. PLACES OF ATTACHMENT OF THE HYPOBRANCHIAL MUSCULATURE IN ANAMNIA

a. The size of the places of attachment

In Pisces

The shape of the hyoid arch in Acanthopterygii is modified in connection with the strong development of the musculus geniohyoideus, which is attached in a concavity of the hyoid arch (Gregory, 1933, p. 231).

In *Opsanus tau* (L.) the ceratohyal and the epihyal bars are stout, probably in connection with the powerful geniohyoid muscles (Gregory, 1933, p. 383).

Perhaps Gregory (1933, p. 300) means the musculus geniohyoideus, when he speaks of the strongly developed muscles of the floor of the mouth in *Stylophorus chordatus* Shaw, which possesses an apparatus acting as a suction trap to drag in the prey. These strong muscles have their origin on the glossohyale and the ceratohyale, which show a large size, perhaps in connection with the size of these muscles.

b. The position

In Pisces

Hyoid arch: in a concavity of it attachment of the musculus geniohyoideus in Acanthopterygii (Gregory, 1933, p. 231); anteriorly on the ceratohyal and epihyal bars probably origin of the musculus geniohyoideus in *Opsanus tau* (L.) (Gregory, 1933, p. 383); on the glossohyale and ceratohyale attachment of the strong suction muscles with which perhaps the musculus geniohyoideus is meant, in *Stylophorus chordatus* Shaw (Gregory, 1933, p. 300).

Branchial arches: on the hyobranchiale III in *Acipenser* and in *Polyodon* and on the hyobranchiale II in *Amia* origin of the musculus branchiomandibularis *s.* geniobranchialis *s.* geniohyoideus (Nishi, 1938, p. 370).

In Amphibia

Lower jaw: near the medial line attachment of the musculus geniohyoideus *s.* rectus superficialis hypobranchialis anterior in Caudata (Nishi, 1938, p. 383).

Tongue bone: attachment of the musculus geniohyoideus *s.* rectus superficialis hypobranchialis anterior in part of the Caudata (Nishi, 1938, p. 383).

Branchial arches: on arcus branchialis II, respectively II and III, attachment of the musculus geniohyoideus *s.* rectus superficialis hypobranchialis anterior in part of the Caudata (Nishi, 1938, p. 383).

The musculi ceratohyoidei in Caudata, lying between the cornu of the tongue bone and arcus branchialis I and the musculus ceratohyoideus in Apoda, lying between the tongue bone and arcus branchialis I, do not belong to this system of muscles (Nishi, 1938, pp. 383, 384).

42. PLACES OF ATTACHMENT OF THE VENTRAL CERVICAL MUSCULATURE IN AMNIOTA

The position

In Reptilia

Occiput: attachment of the musculus cervicoquadratus *s.* retractor ossis quadrati in Serpentes (Nishi, 1938, p. 399).

Quadratum: attachment of the musculus cervicoquadratus *s.* retractor ossis quadrati in Serpentes (Nishi, 1938, p. 399).

Larynx: partial attachment of deeper fascicles of the different muscles, comparable to the musculus sternohyoideus, as is the case with the musculus hyolaryngeus in Serpentes (Nishi, 1938, p. 399); attachments of the musculus geniohyoideus may occur in Reptilia, as the musculus geniolaryngeus in Serpentes shows (Nishi, 1938, p. 399).

Trachea: partial attachment of deeper fascicles of the different muscles, comparable to the musculus sternohyoideus, as is the case with the musculus hyotrachealis in Serpentes (Nishi, 1938, p. 399); attachment of the musculus geniohyoideus may occur in Reptilia, as the musculus geniotrachealis in Serpentes shows (Nishi, 1938, p. 399).

In Aves

Tongue bone: on its corpus attachment of the musculus tracheohyoideus in Picidae (Böker, 1937, pp. 92/93).

Larynx, trachea and syrinx: attachments of the musculus hyolaryngeus, tracheolaryngeus, hyotrachealis, ypsilotrachealis, tracheolaryngeus, a.s.o., parts of the deeper fascicles of the different muscles, comparable to the musculus sternohyoideus, muscles connecting larynx, trachea and syrinx (Nishi, 1938, p. 399); on the trachea, which shows local deformities and processes, attachment of the musculus tracheohyoideus in Picidae (Böker, 1937, pp. 92/93).

In Mammalia

Lower jaw: on its medial area insertion of the musculus geniohyoideus in Mammalia, except in *Ornithorhynchus*; exceptionally this muscle is lacking (*Epomophorus*) (Nishi, 1938, p. 417).

Tongue bone: on its body and on its caudal horn insertion of the musculus thyreohyoideus in Mammalia; this muscle is seldom lacking (*Ornithorhynchus*) (Nishi, 1938, p. 416); on the tongue bone origin of the musculus geniohyoideus, in *Phascolarctos* only partial origin; it is exceptional for this muscle to be lacking (*Epomophorus*) (Nishi, 1938, p. 417); on the cornu hyale and cornu branchiale attachment of the musculus ceratohyoideus, connecting the two cornua; the occurrence of this muscle is rather inconstant in Mammalia; the two cornua hyalia are connected by the musculus hyoideus transversus, which is also inconstant in occurrence in Mammalia (Nishi, 1938, p. 417); on the basihyale attachment of the musculus hyo-epiglotticus, which is equally inconstant in Mammalia (Nishi, 1938, p. 417).

Larynx: on the dorsal parts of the laminae of the cartilago thyreoides origin of the musculus thyreohyoideus in Mammalia, perhaps indicated by a line or crista obliqua (Göppert, 1937, p. 837); on the cartilago thyreoides and sometimes also on the cartilago cricoidea (*Myrmecophaga*) origin of the musculus thyreohyoideus in Mammalia (Nishi, 1938, p. 416); this muscle is seldom lacking (*Ornithorhynchus*); on the cartilago cricoidea displacement of attachment in aberrant cases in numerous Mammalia and in human varieties (Nishi, 1938, p. 416); on the cartilago thyreoides partial origin of the musculus geniohyoideus in *Phascolarctos* (Nishi, 1938, p. 417).

Epiglottis: attachment of the musculus hyoepiglotticus, which is inconstant in occurrence in Mammalia (Nishi, 1938, p. 417).

Trachea: attachment of displacements of the musculus thyreohyoideus in numerous Mammalia and in human varieties (Nishi, 1938, p. 416).

43. PLACES OF ATTACHMENT OF THE TONGUE MUSCULATURE

The position

In Reptilia

Lower jaw: on the caudal angle of the chin origin of the musculus genioglossus (Nishi, 1938, p. 448).

Tongue bone: on its cornu branchiale main origin of the musculus hyoglossus; on the basihyale and on the os entoglossum partial insertion of the musculus hyoglossus and the musculus genioglossus (Nishi, 1938, p. 448).

44. PLACES OF ATTACHMENT OF THE GENERAL VISCERAL MUSCULATURE IN MARSIPOBRANCHII

The position

In Myxinoidea

α. Places of attachment of muscles, innervated by the nervus trigeminus

Basal plate skeleton: on its rostral part origin of the musculus basalitentaculo-labialis (Luther, 1938, p. 474); on the dorsal end of its outer lamella and on the soft cartilage in front of it partial insertion of the musculus subnasali-basalis (Luther, 1938, p. 474); on the lateral margin of the outer lamella of its rostral segment insertion of the musculus craniobasalis;

more rostralwards and on its middle segment insertion of some fibres of this muscle (LUTHER, 1938, p. 474); on the ventral carina of its caudal segment partial origin of the lateral head of the musculus protractor dentium profundus and oralwards of the latter in the region of its caudal segment origin of the medial head of the musculus protractor dentium profundus (LUTHER, 1938, p. 475); on the dorsal margin of its most caudal segment origin of the musculus protractor dentium superficialis (LUTHER, 1938, p. 475); on its inner portion, ventrally, lateral of the midline and up to this line between the rostral edge and the medial fenestra, insertion of the musculus levator cartilaginis basalis (LUTHER, 1938, p. 476).

Trabecula: partial origin of the musculus trabeculosubnasalis superficialis (LUTHER, 1938, p. 472); on the lateroventral surface of its rostral part, just behind the transition into the cornual cartilage, insertion of the musculus flexor trabeculae (LUTHER, 1938, p. 474); partial origin of the musculus craniovelaris (LUTHER, 1938, p. 476).

Cornual cartilage: on its dorsomedial surface, on about the caudal $^2/_3$, insertion of the musculus trabeculosubnasalis profundus (LUTHER, 1938, p. 472); on its side origin of the musculus levator cartilaginis basalis (LUTHER, 1938, p. 476).

Orbital region: on the membranous cranial capsule, closely behind or above the eye, partial origin of the musculus craniobasalis (LUTHER, 1938, p. 474).

Nasal tube: on its wall partial insertion of the musculus nasalis (LUTHER, 1938, p. 472); on its most rostral ring insertion of the musculus subnasalinasalis (LUTHER, 1938, p. 473).

Nasal capsule: on its rostral half partial origin of the musculus nasalis (LUTHER, 1938, p. 472); partial origin of the musculus trabeculosubnasalis superficialis (LUTHER, 1938, p. 472).

Hypophysal plate: partial origin of the musculus craniovelaris (LUTHER, 1938, p. 476).

Cartilago subnasalis: on its lateral surface, on its middle part or a little in front of it, insertion of the musculus trabeculosubnasalis superficialis (LUTHER, 1938, p. 472); on its lateral surface, about on the caudal $^2/_3$, origin of the musculus trabeculosubnasalis profundus (LUTHER, 1938, p. 472); on the rostro-ventral processus for the larger part origin of the musculus subnasali-nasalis (LUTHER, 1938, p. 473); on its lateral surface partial origin of the musculus subnasali-basalis (LUTHER, 1938, p. 474).

Chondroidal bar: on the so-called "superior chondroidal bar" and on the most caudal end of the so-called "inferior chondroidal bar" origin of the musculus clavatus, constituting the nucleus of the so-called club-shaped muscle (LUTHER, 1938, p. 475); on the so-called "superior chondroidal bar" and on the "inferior chondroidal bar" attachments of the musculus perpendicularis, extending between these two bars (LUTHER, 1938, p. 476).

Arcus subocularis: on its inner surface origin of the musculus flexor trabeculae (LUTHER, 1938, p. 474); partial origin of the musculus craniobasalis (LUTHER, 1938, p. 474); partial origin of the musculus craniovelaris (LUTHER, 1938, p. 476).

Branchial arch: on the first arch and on the ventral trunc of the pharyngeal skeleton partial origin of the musculus craniobasalis (LUTHER, 1938, p. 474).

Tentacular cartilages: on the inner process of the support of the tentacular cartilage I and III partial insertion of the musculus nasalis (Luther, 1938, p. 472); on the support of the tentacular cartilage I and III insertion of a caudal portion of the musculus basali-tentaculo-labialis and of a portion that moves the third tentacle (Luther, 1938, p. 474); on the ventrolateral side of the tentacular cartilage II insertion of the marginal portion of the musculus basali-tentaculo-labialis, the so-called musculus tentacularis anterior (Luther, 1938, p. 474); on the dorsal side of the support of the tentacular cartilage I and III, closely behind the origin of the tentacular cartilage III, origin of the musculus coronarius (Luther, 1938, p. 474); on the tentacular cartilage III, closely behind its processus internus, insertion of the musculus coronarius (Luther, 1938, p. 474).

Tooth-plate sketelon: insertion of the lateral and the medial head of the musculus protractor dentium profundus, of the musculus protractor dentium superficialis and of the musculus clavatus (Luther, 1938, p. 475).

Velar cartilage: insertion of the musculus craniovelaris (Luther, 1938, p. 476).

β. Places of attachment of muscles, innervated by the nervus facialis

Basal plate: on the ventrolateral surface of its rostral outer lamella, ventrally of the musculus craniohyoideus, partial insertion of the musculus protractor cartilaginis basalis anterior; ventrally on its middle portion partial insertion of the musculus protractor cartilaginis basalis anterior (Luther, 1938, p. 477); on the dorsal margin of its caudal segment partial insertion of the musculus protractor cartilaginis basalis posterior (Luther, 1938, p. 478).

Ear capsule: on its caudal surface main origin of the musculus craniohyoideus, some fibres of the latter originate from the caudal edge of the bridge of soft cartilage between the ear capsule and the first pharyngeal arch (Luther, 1938, p. 477).

Cornual cartilage: caudally of the musculus levator cartilaginis basalis partial origin of the musculus protractor cartilaginis basalis anterior (Luther, 1938, p. 477).

Arcus subocularis: partial origin of the musculus protractor cartilaginis basalis posterior (Luther, 1938, p. 478).

Pharyngeal skeleton: on the outer surface of the pharyngeal arch II, closely in front of its fusion with the basal plate, insertion of the musculus craniohyoideus (Luther, 1938, p. 477); on pharyngeal arch II, between the musculus craniohyoideus and the musculus retractor mucosae oris (laterally from this) partial insertion of about a third part of the fibres of the musculus protractor cartilaginis basalis anterior (Luther, 1938, p. 477).

γ. Places of attachment of muscles, innervated by the nervus glossopharyngeus

Skull (without detailed indication): close behind the ear capsule origin of the musculus constrictor pharyngis (Luther, 1938, p. 478).

Basal plate: on the dorsolateral margin of its caudal part main insertion of the musculus constrictor pharyngis (Luther, 1938, p. 478).

Pharyngeal skeleton: on the caudal margin of the ventral end of pharyngeal arch II insertion of one of the portions of the musculus constrictor pharyngis, some fibres insert on the root of pharyngeal arch III (LUTHER, 1938, p. 478).

In Petromyzonidae

α. Places of attachment of muscles, innervated by the nervus trigeminus

Basal plate: on the cranial base, *i.e.* on the medial edge of the cranial rod in the caudal part of the fenestra basicranialis *s.* hypophyseos origin of the musculus craniovelaris (LUTHER, 1938, p. 484).

Cartilago tectoria: on its inner surface, close to the middle line, origin of the musculus tectolateralis (LUTHER, 1938, p. 480); on its surface origin of the musculus tectospinosus anterior (LUTHER, 1938, p. 481); on its caudal margin insertion of the musculus tectomandibularis (LUTHER, 1938, p. 482).

Cartilago annularis: on its lateral circumference oral attachment of the musculus anuloglossus (LUTHER, 1938, p. 483).

Cartilago apicalis: rostralward insertion of the musculus cardio-apicalis (LUTHER, 1938, p. 481).

Cartilago spinosa: on its outer surface insertion of the musculus tectospinosus anterior and posterior (LUTHER, 1938, p. 481); on its medial margin insertion of the musculus spinosocopularis (LUTHER, 1938, p. 481).

Cartilago copularis: ventrally on its transverse rod origin of the musculus spinosocopularis (LUTHER, 1938, p. 481).

Cartilago lateralis: partial insertion of the musculus tectolateralis (LUTHER, 1938, p. 480); on its surface origin of the musculus tectospinosus posterior (LUTHER, 1938, p. 481).

Cartilago glossa: on its ventral margin aboral attachment of the musculus anuloglossus (LUTHER, 1938, p. 483).

Pars styloidea mandibularis: on its rostral circumference origin of the musculus tectomandibularis (LUTHER, 1938, p. 482); on its caudal side near its base origin of the musculus mandibulovelaris descendens (LUTHER, 1938, p. 483).

Pars cornualis mandibularis: on its base, immediately rostralward of the place of origin of the musculus mandibulari-apicalis, origin of the musculus mandibulovelaris ascendens (LUTHER, 1938, p. 483).

Hypobranchial longitudinal bar: partial origin of the musculus cardio-apicalis (LUTHER, 1938, p. 481).

Velar cartilage: insertion of a few fibres of the musculus mandibulovelaris descendens (LUTHER, 1938, p. 483); on its inner surface insertion of the musculus mandibulovelaris ascendens (LUTHER, 1938, p. 483); on its outer side insertion of the musculus craniovelaris (LUTHER, 1938, p. 484).

β. Places of attachment of muscles, innervated by the nervus facialis, the nervus glossopharyngeus and the nervus vagus

Cartilago annularis: dorsally origin and ventrally insertion of the more caudal and deeper portion of the musculus sphincter branchialis externus, portio anterior; this ring is broadened to a plate where the muscle adjoins it (LUTHER, 1938, pp. 486/487).

Hypochordal longitudinal bar: dorsally partial origin of the pars posterior of those parts of the musculus constrictor branchialis externus which are innervated by the nervus glossopharyngeus and by the nervus vagus (LUTHER, 1938, p. 486); closely rostralward of the upper end of its branchial arch origin of the musculus adductor branchialis dorsalis (LUTHER, 1938, p. 486).

Ventral longitudinal bar: insertion of the pars posterior of those parts of the musculus constrictor branchialis externus which are innervated by the nervus glossopharyngeus and by the nervus vagus (LUTHER, 1938, p. 486); origin of the musculus adductor branchialis ventralis (LUTHER, 1938, p. 486).

Epibranchial longitudinal bar: partial insertion of the musculus adductor branchialis dorsalis (LUTHER, 1938, p. 486); attachment of the more rostral and superficial portion of the musculus sphincter branchialis externus, portio anterior (LUTHER, 1938, p. 486); attachment of the musculus sphincter branchialis externus posterior (LUTHER, 1938, p. 487).

Hypotremal longitudinal bar: partial insertion of the musculus adductor branchialis ventralis (LUTHER, 1938, p. 486).

Hypobranchial longitudinal bar: attachment of the more rostral and superficial portion of the musculus sphincter branchialis externus, portio anterior (LUTHER, 1938, p. 486); attachment of the musculus sphincter branchialis externus posterior (LUTHER, 1938, p. 487).

Branchial arches: on their caudal dorsal process as a rule partial origin of one or a few most caudal fibres of the pars posterior of those parts of the musculus constrictor branchialis externus which are innervated by the nervus glossopharyngeus and by the nervus vagus (LUTHER, 1938, p. 486); on their most ventral rostral process insertion of some most caudal fibres of the pars posterior of those parts of the musculus constrictor branchialis externus which are innervated by the nervus glossopharyngeus and by the nervus vagus (LUTHER, 1938, p. 486); partial insertion of the musculus adductor branchialis dorsalis (LUTHER, 1938, p. 486); partial insertion of the musculus adductor branchialis ventralis (LUTHER, 1938, p. 486).

45. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE MANDIBULAR ARCH IN PISCES

a. Introduction

The musculature of the mandibular arch in Pisces contains the muscles of the upper jaw, which, in many cases, is movable and even protrusile to a high degree, and the muscles for the lower jaw. The muscles for the operculum also belong to them.

A number of facts about the relations between the development of the musculus constrictor I ventralis, of the musculus adductor mandibulae and of the musculus praeorbitalis and certain characters of the skull and head are known. Perhaps the investigation of these relations will give us information about the relation between the size of the place of attachment of these muscles and its position, and the elements of the skull and head mentioned.

In literature we found the following remarks about a relation between the development of these muscles and their places of attachment.

There is a relation in Selachii between the development of the musculus constrictor 1 dorsalis and the size of the spiraculum and the length of the slit of the mouth in a longitudinal direction (LUTHER, 1938, pp. 494/495). The development of the musculus praeorbitalis shows a relation with the length, breadth and position of the slit of the mouth in Selachii (LUTHER, 1938, pp. 501, 502), with the position of the jaw apparatus in Selachii (LUTHER, 1938, p. 502) and with the size of the eye (LUTHER, 1938, p. 502), with the far rostral position of the jaw joint in Holocephali (LUTHER, 1938, p. 505) and with the immovability of the palatoquadratum in Holocephali (LUTHER, 1938, p. 505). There is a relation between the development of the musculus praeorbitalis and also of the musculus adductor mandibulae and the development of the dentition in Holocephali (LUTHER, 1938, p. 505). There is a relation between the development of the muscles attached to the accessory premandibular cartilage in *Callorhynchus* and the position of its rostrum and mouth (LUTHER, 1938, p. 507) and between the development of the muscles attached to the labial cartilages in *Chimaera* and the position of its rostrum and jaw apparatus (LUTHER, 1938, p. 507). There is a relation between the development of the musculus protractor hyomandibularis in Chondrostei and the development of the protrusibility of the jaw apparatus (LUTHER, 1938, pp. 508, 509). There is a relation between the development of the musculus adductor mandibulae and the development of the dentition in Selachii (LUTHER, 1938, p. 500) and the development of the dentition and of the jaws in certain plankton-eating Chondrostei as *e.g. Polyodon* (LUTHER, 1938, p. 509) and the development of the dentition in Dipneusta (LUTHER, 1938, p. 515). There is a relation between the development of the musculus dilatator operculi in Teleostei and the reduction of the spiraculum (LUBOSCH, 1938, p. 1011).

b. The size

A number of facts about the size of the lateral temporal groove or fossa, in which the origin of the musculus dilatator operculi lies, are given by Gregory (1933).

In *Tarpon atlanticus* (C. & V.) it is conspicuous and a well marked depression or fossa (Gregory, 1933, pp. 141, 245), in *Gonorhynchus greyi* Clark it is a narrow groove (Gregory, 1933, p. 178), in *Holocentrus ascensionis* (Osbeck) it is a prominent fossa (Gregory, 1933, p. 237), in *Luciolates* very narrow (Gregory, 1933, p. 245), in *Cirrhites* large and sharply defined (Gregory, 1933, p. 259) and a small but distinct fossa in *Astroscopus y-graecum* (C. V.), in which the mobility of the operculum is slight (Gregory, 1933, p. 370).

c. The position

Cerebral skull (without detailed indication): the endocranial vault or braincase proper generally affords support to the often powerful muscles that operate the opercular flap in Pisces (Gregory, 1933, p. 435).

Ventral side of the skull: doubtless origin of the musculus praeorbitalis in Squalidae (Spinacidae), which shows a more ventral origin, in connection with the inclination of the jaw apparatus (Luther, 1938, p. 502); ventromedial of the orbita origin of the musculus praeorbitalis in Batoidei (Luther, 1938, p. 502); on the neurocranium ventral (and in front) of the eye origin of the musculus praeorbitalis in Holocephali (Luther, 1938, p. 505); on the cranium ventral of the orbita in the region of the palatoquadratum, which is fused to the neurocranium, origin of the musculus adductor mandibulae in Holocephali (Luther, 1938, p. 505).

Lateral wall of the neurocranium: on the ossified lateral wall of the skull partial origin of the musculus levator arcus palatini in Teleostei (Lubosch, 1938, p. 1011); on the neurocranium in front of the hyomandibulare and as far rostralward as the parabasale extends partial insertion of the musculus parabasalis in *Amia* (Luther, 1938, p. 512); on the neurocranium and the covering bones partial origin of the musculus adductor mandibulae in later ontogenetic stages of *Amia* (Luther, 1938, p. 513).

Lateral surface of the skull: in a fossa on the skull partly dorsally covered by dermal bones, beginning on the dorsal side of the eye and extending to the hyomandibulare, origin of the musculus protractor hyomandibularis, which is a strong muscle in *Acipenser* and in *Scaphirhynchus* (Luther, 1938, p. 508); in the depth of the lateral wall of the skull partial origin of the more feebly developed musculus protractor hyomandibularis in *Polyodon* (Luther, 1938, p. 509).

Regio otica: on the labyrinth region origin of the musculus constrictor 1 dorsalis in Selachii (Luther, 1938, p. 494); rostralward of the foramen nervi VII, so no doubt on the otic region, origin of the musculus levator palatoquadrati in *Pristis* (Luther, 1938, p. 497); on the labyrinth region dorsalward of the foramen nervi VII origin of one portion, in front and ventralward in front of the foramen nervi VII (*Trygon*, *Rhynchobatus*) or more caudalward (*Rhinobatus*, *Raja*) origin of the other, deeper portion of the musculus levator palatoquadrati (Luther, 1938, p. 497); shifted towards the dorsal surface of the skull, but probably still on the labyrinth region, origin of the dorsal portion of the musculus levator palatoquadrati in Torpedinidae (the other portion is lacking), to a lesser degree in *Narke* (*Astrape*) as far as the neighbourhood of the middle line in *Torpedo* (Luther, 1938, p. 497); dorsalward shifted, but probably still on the otic region, origin of the musculus levator palatoquadrati in *Mitsukurina* among the Lamnidae (by this a larger height of lift in accordance with the extreme protrusibility of the jaw apparatus is attained) (Luther, 1938, p. 497); markedly dorsalward extension, but probably still on the otic region, of the origin of the musculus levator palatoquadrati in many Carcharhinidae, in *Eulamia* (*Carcharias*) transgressing upon the processus postorbitalis (Luther, 1938, p. 497); no origin on it of the musculus constrictor 1 dorsalis in Holocephali, as this muscle is lacking in connection with the fact that neurocranium and palatoquadratum are fused and the spiraculum is lacking (Luther, 1938, p. 505); no origin on it of the musculus constrictor 1 dorsalis in Dipneusta, as this muscle is lacking in connection with the fact that there is no movability between palatoquadratum and neurocranium (Luther, 1938, p. 515); on the cartilaginous skull from the orbita to the caudal upper bump of the skull partial origin of the musculus adductor mandibulae in *Neoceratodus* (Luther, 1938, pp. 515/516); on the cartilaginous and osseous neurocranium, probably in the same region, partial origin of the musculus adductor mandibulae internus in Lepidosireniformes (Dipneumones) (Luther, 1938, p. 517); on the cartilaginous skull, on the otica, partial origin of the musculus praeorbitalis superficialis in *Lepisosteus* (Luther, 1938, p. 514); on the skull wall, perhaps on the regio otica, partial origin of the musculus praeorbitalis profundus in *Lepisosteus* (Luther, 1938, p. 514).

Cheek armour: partial origin of the superficial layer and of the middle layer of the musculus adductor mandibulae, the so-called musculus maxillaris and musculus mandibularis, in Teleostei; the middle layer can extend on its origin as far as the roof of the skull (*Esox*, *Anarhichas*, *Onos* (*Motella*), Cottoidei (Scleroparei)), sometimes even left and right muscles meet dorsally (*Anguilla*) (Lubosch, 1938, p. 1012). Perhaps the cheek plates, called postorbitalia, which according to Gregory (1933, p. 89) laterally cover the musculus adductor mandibulae in Semionotidae, *Lepisosteus*, primitive Amioidae, *etc.*, also bear part of the origin of this muscle.

Squamosum, pteroticum and sphenoticum: on the squamosum origin of the musculus dilatator operculi in *Amia* (Luther, 1938, p. 512); on the squamosum main origin of the musculus dilatator operculi in Teleostei (Lubosch, 1938, p. 1011); on the dorsolateral surface of the sphenoticum or above the postorbital process of the sphenoticum lies the fossa for the musculus dilatator operculi in *Tarpon atlanticus* (C. & V.) (Gregory, 1933, pp. 141, 245); on the lateral edge of the sphenoticum and pteroticum above the hyomandibulare lies this fossa in *Gonorhynchus greyi* Clark (Gregory, 1933, p. 178); beneath the dermal roof of the sphenoticum and pteroticum lies this fossa in *Astroscopus y-graecum* (C. V.) (Gregory, 1933, p. 370). We add the following remarks about the position of this fossa here: in *Holocentrus ascensionis* (Osbeck) it lies on the cranial roof above the hyomandibular facet (Gregory, 1933, p. 237), in *Luciolates* the nearly horizontal fossa lies chiefly on the lateral border of the pteroticum immediately above the elongate glenoid cavity of the hyomandibulare (Gregory, 1933, p. 245) and in *Cirrhites* the fossa lies above the postorbital bar (Gregory, 1933, p. 259). On the sphenoticum partial origin of the musculus levator arcus palatini in Teleostei (Lubosch, 1938, p. 1011); on the squamosum partial origin of the musculus adductor mandibulae in *Neoceratodus* (Luther, 1938, p. 516); on the squamosum main origin of the musculus adductor mandibulae posterior in Lepidosireniformes (Dipneumones) (Luther, 1938, p. 517); on the inner side of the squamosum partial origin of the musculus praeorbitalis superficialis in *Lepisosteus* (Luther, 1938, p. 514).

Parietale, frontoparietale, postfrontale, postorbitale and frontale: on the postfrontale and frontale origin of the musculus constrictor 1 dorsalis in Crossopterygii (Luther, 1938, p. 511); on the postfrontale origin of the musculus levator arcus palatini in *Amia* (Luther, 1938, p. 512); on the inner side of frontale and postfrontale as well as on the adjacent supraorbital part of the cartilaginous skull origin of the musculus adductor mandibulae medius in Crossopterygii (Luther, 1938, p. 512); on the inner side of the osseous cranial roof for the greater part on the frontoparietale, postfrontale and supraorbitale partial origin of the musculus adductor mandibulae in *Neoceratodus* (Luther, 1938, p. 516); on the inner side of parietale and frontale partial origin of the musculus praeorbitalis superficialis in *Lepisosteus* (Luther, 1938, p. 514); on the osseous neurocranium, a.o. on the dorsal side of the frontoparietale partial origin of the musculus adductor mandibulae internus in Lepidosireniformes (Dipneumones) (Luther, 1938, p. 517).

Tenaculum: on its rostral part origin of a part of the fibres of the musculus praeorbitalis in the male Holocephali (Luther, 1938, p. 505).

Praefrontale and processus praefrontalis: on the processus praefrontalis partial origin of the musculus praeorbitalis in *Amia* (Luther, 1938, p. 513); on the praefrontale *s.* antorbitale insertion of the musculus nasalis in *Amia* (Luther, 1938, p. 513).

Orbitosphenoid, septum interorbitale and parasphenoid: on the orbitosphenoid and on the parasphenoid, partly ventral of the foramen rami 1 nervi trigemini ($N\,V_1$), origin of the musculus adductor mandibulae internus in Crossopterygii (Luther, 1938, p. 512); on the cartilaginous, osseous and membranaceous septum interorbitale partial origin of the musculus praeorbitalis superficialis in *Lepisosteus* (Luther, 1938, p. 514); on the septum interorbitale downward as far as the parasphenoid partial origin of the musculus praeorbitales profundus in *Lepisosteus* (Luther, 1938, p. 514); on the lateral side of the parasphenoid origin of the musculus adductor arcus palatini in higher Pisces (Gregory, 1933, p. 435).

Processus postorbitalis: partial origin of the musculus levator arcus palatini in Teleostei (Lubosch, 1938, p. 1011); partial origin of the musculus adductor mandibulae γ in Hexanchidae (Notidanidae) and *Oxynotus* (*Centrina*) (Luther, 1938, p. 500); medial of the eye partial origin of the musculus protractor hyomandibularis in *Polyodon* (Luther, 1938, p. 509).

Processus praeorbitalis: partial origin of the musculus adductor mandibulae lateralis 2 in Rhinobatidae and in *Raja* (Luther, 1938, p. 501); partial origin of the musculus praeorbitalis in the asterospondylic sharks (Scyliorhinidae, Carcharhinidae) (Luther, 1938, pp. 501/502).

Roof of the skull above the orbita: from the ethmoidal region extending over the roof of the orbita as far as the fossa parietalis origin of the musculus praeorbitalis in *Chiloscyllium* and in *Stegostoma* (LUTHER, 1938, p. 502).

Ethmoidal region: on the caudal side of the nasal capsule partial insertion of the musculus protractor hyomandibularis (LUTHER, 1938, p. 509); on the nasal capsule or ventral of it rostralward partial origin of the musculus adductor mandibulae γ in *Chiloscyllium*, *Heterodontus* and *Heptranchias* (*Heptanchus*) (LUTHER, 1938, p. 500); on the neurocranium rostral of the eye origin of the musculus praeorbitalis in Selachii, where this muscle is seldom lacking (*Squatina*, Torpedinidae and *Myliobatis*) (LUTHER, 1938, p. 501); no origin on the cartilage in *Isurus* (*Lamna*) (LUTHER, 1938, p. 502); on the caudal part of the nasal capsule partial origin of the musculus praeorbitalis in asterospondylic sharks (Scyliorhinidae, Carcharhinidae) (LUTHER, 1938, pp. 501/502); on the neurocranium ventrally and in front of the eye origin of the musculus praeorbitalis in Holocephali (LUTHER, 1938, p. 505).

Parethmoidal cartilage: partial origin of the rostral portion of the musculus adductor mandibulae in Rhinobatidae (LUTHER, 1938, p. 501).

Caudal prolongation of the saw: on the teeth-bearing zygomatic-arch-like bar which constitutes a caudal prolongation of the saw origin of the feebly developed musculus adductor mandibulae which for the greater part consists of the musculus adductor γ in *Pristiophorus* (LUTHER, 1938, p. 500).

Maxillare, praemaxillare and rostrale: on the maxillare insertion of the superficial layer of the musculus adductor mandibulae, the so-called musculus maxillaris, or of two separate parts of this muscle, in Teleostei for which this insertion is new among Pisces (LUBOSCH, 1938, pp. 1012, 1013, 1014; see also GREGORY, 1933, p. 425); the insertion of one of these parts may be shifted on the praemaxillare and even on the rostrale (LUBOSCH, 1938, p. 1013); also the deep layer of the musculus adductor mandibulae, the so-called musculus mandibularis, may be connected with the maxillare in some Teleostei (LUBOSCH, 1938, p. 1014).

Labial cartilages: on the ventral or mandibular one insertion of a fascicle of the ventral part of the musculus adductor mandibulae in *Chlamydoselachus* (LUTHER, 1938, pp. 498/499); a similar insertion in *Echinorhinus* (LUTHER, 1938, p. 499); on the labial cartilage partial attachment of the musculus praeorbitalis in some Squaliformes (*Heterodontus*, *Pristiurus melastomus* (Raf.), *Mitsukurina*, *Mustelus mustelus* (L.) (*Mustelus laevis*)) (LUTHER, 1938, p. 505); on the prelabial cartilage insertion of the musculus levator cartilaginis praelabialis in Holocephali (LUTHER, 1938, p. 506); on the most rostral part of the maxillar cartilage insertion of the musculus levator anguli oris anterior in Holocephali (LUTHER, 1938, p. 506); on the maxillar cartilage and on the accessory mandibular cartilage attachment of the musculus levator anguli oris posterior in Holocephali (LUTHER, 1938, p. 506); the rostral part of the prelabial cartilage is connected with the rostral end of the (rostral) maxillar cartilage by the musculus labialis anterior in Holocephali (LUTHER, 1938, pp. 506/507); from the maxillar cartilage to the caudal process of the accessory premandibular cartilage runs the musculus labialis posterior (LUTHER, 1938, p. 507); on the caudal part of the accessory premandibular cartilage, on which it extends lateralward and especially medialward, insertion of the musculus labialis inferior in Holocephali (LUTHER, 1938, p. 507).

Palatoquadratum: on its dorsal margin or on the dorsal part of its inner surface insertion of the musculus constrictor 1 dorsalis in Selachii (Luther, 1938, p. 494); in the region of the processus muscularis or a little in front of it insertion of the musculus levator palatoquadrati in Selachii (Luther, 1938, p. 497); shifted towards the symphysis partial insertion of this muscle in Batoidei (Luther, 1938, p. 497); in the neighbourhood of the symphysis partial insertion of the musculus levator palatoquadrati in *Pristis* and in the same way of the two portions of this muscle in other Batoidei; in other Batoidei again extension up to the symphysial middle line of the insertion of these two portions which are here sometimes fused (*Trygon*, *Myliobatis*) (Luther, 1938, p. 497); far articularwards insertion of the musculus levator palatoquadrati in Sphyrnidae, so the other extreme of the condition in many Batoidei which show a symphysial fusion of left and right muscles (Luther, 1938, pp. 497/498); no insertion of the musculus constrictor 1 dorsalis in Holocephali, as this muscle is lacking in connection with the fact that neurocranium and palatoquadratum are fused and the spiraculum is lacking (Luther, 1938, p. 505); on the cartilaginous quadratum partial insertion of the musculus constrictor 1 dorsalis, of the so-called musculus levator arcus palatini, in Crossopterygii (Luther, 1938, p. 511); on the metapterygoid for the greater part insertion of the musculus levator arcus palatini in *Amia* (Luther, 1938, p. 512); on the metapterygoid partial insertion of the musculus levator arcus palatini in Teleostei (Lubosch, 1938, p. 1011); on the palatoquadratum origin of the musculus adductor mandibulae in Selachii (Luther, 1938, p. 494); this muscle filling up the muscular grooves in the jaws in *Chlamydoselachus* (Luther, 1938, p. 498); far articularward on the palatoquadratum origin of the musculus adductor γ in many Squaliformes (Luther, 1938, p. 500); on the outer surface and the abdental margin of the palatoquadratum and a little on its medial side origin of the musculus adductor mandibulae lateralis 1 in *Pristis* (Luther, 1938, pp. 500/501); on the palatoquadratum origin of the musculus adductor mandibulae medialis in *Myliobatis* in the neighbourhood of the symphysis, whereas in *Trygon* the symphysial quarter part of it is left free (Luther, 1938, p. 501); on a strong process of the palatoquadratum origin of a rostral portion of the musculus adductor mandibulae in Rhinobatidae (Luther, 1938, p. 501); on the palatoquadratum symphysialward origin of this rostral portion of the musculus adductor mandibulae, more articularwards origin of the musculus adductor γ and still more caudalward muscular fibres on the palatoquadratum in *Raja* (Luther, 1938, p. 501); on the pars palatina origin of the symphysial portion and on the pars quadrata of the articular portion of the musculus adductor mandibulae in *Polyodon* (Luther, 1938, p. 509); on the symphysial and dorsal margin of the palatoquadratum origin of the symphysial portion and on the pars quadrata but for the greater part on the praemaxillare or praemaxillo-maxillo-palatinum origin of the articular portion of the musculus adductor mandibulae in *Acipenser* and *Scaphirhynchus* (Luther, 1938, p. 509); on the cartilaginous and osseous quadratum and on the metapterygoid partial origin of the musculus adductor mandibulae externus in Crossopterygii (Luther, 1938, p. 511); on the palatinum partial origin of the musculus praeorbitalis in *Amia* (Luther, 1938, p. 513); on the palatinum insertion of the musculus nasalis in *Amia* (Luther, 1938, p. 513); on the palatoquadratum only origin of the musculus adductor mandibulae in young ontogenetic stages of *Amia* (LUTHER, 1938, p. 513); on the bones and on the cartilage of the pterygoquadrate row partial origin of the musculus adductor mandibularis *s.s.* in *Lepisosteus* (LUTHER, 1938, p. 514); on the cartilaginous palatoquadratum, on the quadratum and on the dermopalatinum origin of the musculus palatomandibularis major and on the palatoquadratum origin of the musculus palatomandibularis minor in *Lepisosteus* (LUTHER, 1938, p. 515); on the quadratum partial origin of the musculus adductor mandibulae in *Neoceratodus* (LUTHER, 1938, pp. 515/516); on all elements of the suspensorium origin of the different layers of the musculus adductor mandibulae in Teleostei (LUBOSCH, 1938, p. 1012); on the metapterygoid (quadratum) or on the arcus palatoquadratus partial origin of the deep layer of the musculus adductor mandibulae or of the so-called musculus mandibularis in Teleostei (LUBOSCH, 1938, p. 1012); on the same places partial origin of the superficial layer and of the middle layer of the musculus adductor mandibulae, the so-called musculus maxillaris and musculus mandibularis in Teleostei (LUBOSCH, 1938, p. 1012); on the oblique antero-lateral faces of the suspensorium attachment of the powerful musculus adductor mandibulae in *Opsanus tau* (L.) (GREGORY, 1933, p. 383); on the outer surface of the metapterygoid partial attachment of the musculus adductor mandibulae in Teleostei (GREGORY, 1933, p. 427); on the symplecticum partial origin of the superficial layer and of the middle layer of the musculus adductor mandibulae, the so-called musculus maxillaris and musculus mandibularis, in Teleostei (LUBOSCH, 1938, p. 1012); on the inner side of the arcus palatoquadratus origin of the musculus quadrato-mandibularis internus in some Teleostei such as *Scarichthys* (LUBOSCH, 1938, p. 1014); on the inner surface of the arcus palatoquadratus origin of the symphysial portion of the musculus adductor mandibulae, the so-called musculus mentalis in Teleostei (LUBOSCH, 1938, p. 1014).

Lower jaw: on the mandibulare insertion of the musculus adductor mandibulae in Selachii (LUTHER, 1938, p. 494); this muscle filling up the muscular grooves in the jaws in *Chlamydoselachus* (LUTHER, 1938, p. 498); far articularward insertion of the musculus adductor γ in many Squaliformes (LUTHER, 1938, p. 500); on the abdental margin of the mandibulare insertion of the musculus adductor mandibulae lateralis 1 and near the dental margin of the lower jaw insertion of the musculus mandibulae medialis in *Pristis* (LUTHER, 1938, p. 501); on the lower jaw insertion of the musculus adductor mandibulae medialis in *Myliobatis* in the neighbourhood of the symphysis, whereas in *Trygon* the symphysial quarter part of the lower jaw is left free (LUTHER, 1938, p. 501); on the abdental margin of the mandibulare insertion of the musculus adductor mandibulae lateralis 1 and on the mandibulare insertion of the musculus adductor mandibulae lateralis 2 in Rhinobatidae and in *Raja* (LUTHER, 1938, p. 501); on a retro-articular process of the mandibulare insertion of a portion of the musculus adductor mandibulae in Rhinobatidae (LUTHER, 1938, p. 501); on the lower jaw insertion of the musculus adductor mandibulae in Holocephali (LUTHER, 1938, p. 505); on the cartilaginous mandibulare for the greater part insertion of both portions of the musculus adductor mandibulae in *Polyodon*, only a thin superficial layer of fibres of the articular portion inserts on the dentale (LUTHER, 1938, p. 509); on the mandibulare and on the dentale insertion of both portions of the musculus adductor mandibulae in *Acipenser* and *Scaphirhynchus* (Luther, 1938, p. 509); on the processus coronoideus and on the dorsal margin and the inner surface of the angulare *s.* dermarticulare insertion of the musculus adductor mandibulae externus in Crossopterygii (Luther, 1938, p. 511); on the bottom of the muscular groove of the lower jaw on a small tubercle of the angulare insertion of the musculus adductor mandibulae medius and internus in Crossopterygii (a small section of the tendon runs to the medial side of the processus coronoideus) (Luther, 1938, p. 512); on the cartilage of Meckel insertion of the musculus adductor mandibulae intramandibularis in Crossopterygii (Luther, 1938, p. 512); on the cartilage of Meckel insertion of all portions of the musculus adductor mandibulae in embryos of *Polypterus* (Luther, 1938, p. 512); on the cartilage of Meckel resp. its ossifications insertion of the musculus praeorbitalis and the musculus parabasalis in Holostei (Luther, 1938, p. 514); on the cartilage of Meckel resp. on the jaw groove insertion of the musculus adductor mandibulae in ontogenetic stages of *Amia* (Luther, 1938, p. 513; Lubosch, 1938, p. 1013 foot note); on the supraangulare and on the cartilage of the lower jaw insertion of the musculus adductor mandibularis *s.s.* in *Lepisosteus* (Luther, 1938, p. 514); on the muscular groove of the lower jaw (cartilage and articulare) insertion of the musculus palatomandibularis major in *Lepisosteus* (Luther, 1938, p. 515); on the supraangulare partial insertion of the musculus palatomandibularis minor in *Lepisosteus* (Luther, 1938, p. 515); on the cartilage of Meckel, on the angulare and on the spleniale insertion of the musculus adductor mandibulae in *Neoceratodus* (Luther, 1938, p. 516); on the processus coronoideus insertion of the musculus adductor mandibulae posterior in Lepidosireniformes (Dipneumones) (Luther, 1938, p. 517); on the lower jaw attachment of the musculus adductor mandibulae in Teleostei (Gregory, 1933, p. 425); on the cartilage of Meckel and on the dentale insertion of the deep layer of the musculus adductor mandibulae, the so-called musculus mandibularis in Teleostei (Lubosch, 1938, p. 1012); on the lower jaw partial insertion of the superficial layer of the musculus adductor mandibulae, the so-called musculus maxillaris, in Teleostei (Lubosch, 1938, pp. 1012, 1013); on the lower jaw partial attachment of the musculus adductor mandibulae in Plectognathi (Lubosch, 1938, p. 1026); on the mandibulare insertion of the musculus praeorbitalis in a number of Selachii, in *Oxynotus* (*Centrina*), *Somniosus*, *Scymnorhinus*, *Raja*, *Trygon* (Luther, 1938, pp. 501, 502); on the mandibulare a little symphysial and ventral of the articulation insertion of a little muscle in *Torpedo* (Luther, 1938, p. 502); on its outer surface insertion of the musculus praeorbitalis in Holocephali (Luther, 1938, p. 505); on the processus coronoideus, on the autocoronale, on the supraangulare and on the articulare insertion of the musculus praeorbitalis superficialis and profundus in *Lepisosteus* (Luther, 1938, p. 514); ventrally in the midst of the mandibulare origin of the musculus labialis inferior in Holocephali (Luther, 1938, p. 507); on the mandibulare in the region of the labial cartilage insertion of the musculus intermandibularis posterior superficialis in *Narke* (*Astrape*) (Luther, 1938, p. 503); on the abdental margin of the lower jaw (more symphysialwards as in *Trygon*) attachment of the musculus intermandibularis posterior superficialis in *Torpedo*, where the pars profunda of this muscle is lacking (Luther, 1938, p. 503).

Hyomandibulare: partial insertion of the musculus constrictor 1 dorsalis of the so-called musculus levator arcus palatini, in Crossopterygii and also of another portion of this muscle in *Polypterus* (LUTHER, 1938, p. 511); partial insertion of the musculus levator arcus palatini in *Amia* (LUTHER, 1938, p. 512); on its medial side insertion of the musculus dilatator operculi in *Amia* and in Holostei in general (LUTHER, 1938, pp. 511, 512); partial origin of the musculus levator arcus palatini in some Cyprinidae as an exception among Teleostei (LUBOSCH, 1938, p. 1011); partial insertion of the musculus levator arcus palatini in Teleostei (LUBOSCH, 1938, p. 1011); partial insertion of the musculus dilatator operculi in Teleostei (LUTHER, 1938, p. 511); on its rostral margin often transgressing on its lateral side insertion of the musculus protractor hyomandibularis in Chondrostei (LUTHER, 1938, pp. 508, 509); partial origin of the musculus adductor mandibulae γ in *Squatina* (LUTHER, 1938, p. 500); on its lateral surface partial origin of the musculus adductor mandibulae externus in Crossopterygii (LUTHER, 1938, p. 511); on its rostrodorsal part partial origin of the musculus parabasalis in *Amia* (LUTHER, 1938, p. 512); partial origin of the musculus adductor mandibulae in later ontogenetic stages of *Amia* (LUTHER, 1938, p. 513); on the hyomandibulare partial origin of the deep layer of the musculus adductor mandibulae or of the so-called musculus mandibularis in Teleostei (LUBOSCH, 1938, p. 1012); in the same place partial origin of the superficial layer and of the middle layer of the musculus adductor mandibulae, the so-called musculus maxillaris and musculus mandibularis in Teleostei (LUBOSCH, 1938, p. 1012); on its caudal surface origin of the musculus intermandibularis posterior superficialis in *Narke* (*Astrape*) (LUTHER, 1938, p. 503).

Hyoid: insertion of the musculus spiracularis in *Torpedo torpedo* (L.) (*Torpedo marmorata*) (LUTHER, 1938, pp. 495/496).

Spiracular cartilage: on its ventral part partial origin of the musculus spiracularis in *Torpedo torpedo* (L.) (*Torpedo marmorata*) (LUTHER, 1938, p. 495); on the third spiracular plate partial insertion of the musculus constrictor 1 dorsalis of the so-called musculus spiracularis in Crossopterygii (LUTHER, 1938, p. 511).

Operculum: partial insertion of the musculus constrictor 1 dorsalis of the so-called musculus opercularis *s.* dilatator operculi in *Calamoichthys* and in *Polypterus* (LUTHER, 1938, p. 511); on its medial dorsal corner insertion of the musculus dilatator operculi in Teleostei (LUBOSCH, 1938, p. 1011); on its inner side partial origin of the musculus adductor mandibulae externus in Crossopterygii (LUTHER, 1938, p. 511); on the interoperculum partial origin of the musculus adductor mandibularis *s.s.* in *Lepisosteus* (LUTHER, 1938, p. 514); on the curved or concave anterior border of the praeoperculum and the area in front of it a fan-like origin of parts of the subdivisions of the musculus adductor mandibulae in Teleostei (GREGORY, 1933, pp. 425, 427, fig. 285); on the praeoperculum partial origin of the deep layer of the musculus adductor mandibulae or of the so-called musculus mandibularis in Teleostei (LUBOSCH, 1938, p. 1012); in the same place partial origin of the superficial layer and of the middle layer of the musculus adductor mandibulae, the so-called musculus maxillaris and musculus mandibularis in Teleostei (LUBOSCH, 1938, p. 1012).

46. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE HYOID ARCH IN PISCES

The position

Skull (without detailed indication): origin of the musculus hyomandibularis in ganoids (Luther, 1938, p. 524); origin of the musculus levator hyoidei in larvae of *Polypterus* (Luther, 1938, p. 525).

Occipital region and regio otica: partial origin of the more ventral fascicle of the dorsal part of the musculus constrictor 2 in the Carcharhinidae *Mustelus* and *Galeorhinus*; this fascicle directly borders upon the spiraculum (Luther, 1938, p. 519).

Regio otica: on the labyrinth region origin of the musculus levator hyomandibularis in typical Batoidei (Luther, 1938, p. 522); on the labyrinth region origin of the musculus adductor hyomandibularis in *Amia* (Luther, 1938, p. 524).

Parasphenoid: partial extension of the origin of the musculus adductor hyomandibularis (musculus adductor arcus palatini) in some Teleostei in those cases where a pars palatina is developed (Lubosch, 1938, p. 1015).

Squamosum: on its top dorsal of the hyomandibular joint origin of the musculus levator operculi in Teleostei (Lubosch, 1938, p. 1015).

Pteroticum: on the concave lower surface of the projecting pteroticum no doubt attachment of the musculus adductor hyomandibularis in *Gonorhynchus greyi* Clark (Gregory, 1933, p. 178).

Praefrontale: partial extension of the origin of the musculus adductor hyomandibularis (musculus adductor arcus palatini) in some Teleostei in those cases where a pars palatina is developed (Lubosch, 1938, p. 1015).

Orbita: on the inner side of the cartilage which borders the orbita, origin of the musculus hyoideus superior in Holocephali (Luther, 1938, p. 523).

Maxillare: insertion of the musculus extensor (abductor) tentaculi in Siluridae (Lubosch, 1938, p. 1015).

Palatoquadratum: attachment of the musculus hyomandibulomandibularis in *Heterodontus* (Luther, 1938, pp. 519/520); insertion of the musculus adductor hyomandibularis (musculus adductor arcus palatini) in embryos of *Salmo*, on the metapterygoid in the adult *Salmo*, on the pars pterygoidea in most Teleostei (Lubosch, 1938, p. 1015; see also Gregory, 1933, pp. 414/415).

Lower jaw: attachment of the musculus interhyoideus in Teleostei (Lubosch, 1938, p. 1016).

Hyomandibulare: on its dorsal side insertion of the united ventral and dorsal fascicles of the dorsal part of the musculus constrictor 2 in the Carcharhinidae *Mustelus* and *Galeorhinus* (Luther, 1938, p. 519); attachment of the musculus hyomandibulomandibularis in *Heterodontus* (Luther, 1938, pp. 519/520); insertion of the musculus levator hyomandibularis in typical Batoidei (Luther, 1938, p. 522); insertion of the musculus retractor hyomandibularis in ganoids (Luther, 1938, p. 524); on its inner side insertion of the musculus adductor hyomandibularis in *Amia* (Luther, 1938, p. 524); on its inner surface partial insertion of the musculus levator operculi, the musculus adductor hyomandibularis and the musculus adductor operculi in Teleostei (Lubosch, 1938, p. 1015).

Hyoid: insertion of the musculus levator hyoidei in larvae of *Protopterus* (LUTHER, 1938, p. 525); on the ceratohyale partial origin of the musculus interhyoideus in Teleostei (LUBOSCH, 1938, p. 1016).

Hypohyale: attachment of the musculus hyohyoideus ventralis (inferior) in Teleostei (LUBOSCH, 1938, p. 1015); partial origin of the musculus interhyoideus in Teleostei (LUBOSCH, 1938, p. 1016).

Opercular cartilage: on the opercular cartilage, consisting of fused radii, insertion of the musculus hyoideus superior in Holocephali (LUTHER, 1938, p. 523).

Operculum: on its inner surface partial insertion of the musculus levator operculi, the musculus adductor hyomandibularis and the musculus adductor operculi in Teleostei (LUBOSCH, 1938, p. 1015).

47. PLACES OF ATTACHMENT OF THE MUSCULATURE OF THE BRANCHIAL ARCHES IN PISCES

a. The size

There is a connection between the development of the musculi adductores arcuum branchialium in *Polyodon* and the remarkable development of the branchial arches serving as a sieving apparatus (LUTHER, 1938, p. 535).

In Cyprinoidei the "subtemporal fossa", which serves for the lodgment of the great muscles which pull up the inferior pharyngeal bones, is large, larger even than in *Tarpon*, where the "subtemporal fossa" is likewise prominently developed and deep and which may also lodge some of the muscles of the branchial apparatus (GREGORY, 1933, pp. 141/142).

b. The position

Skull (without detailed indication): origin of the musculi interbranchiales of arcus branchialis I–IV in *Neoceratodus* (LUTHER, 1938, p. 538); for the greater part origin of the musculi levatores arcuum branchialium in ganoids (LUTHER, 1938, p. 533); origin of one of the two portions of the musculus levator arcus branchialis of arcus branchialis II in *Acipenser ruthenus* L. (LUTHER, 1938, p. 533); on the wall of the skull partial origin of the strongest portion of the musculus levator arcus branchialis of arcus branchialis III in *Acipenser ruthenus* L. (LUTHER, 1938, p. 533); on the chondrocranium origin of the musculi levatores arcuum branchialium of arcus branchialis I–IV in *Polyodon* (LUTHER, 1938, p. 534).

Cerebral skull (without detailed indication): the endocranial vault or brain case proper generally affords support to muscles that operate the branchial apparatus in Pisces (GREGORY, 1933, p. 435).

Basis cranii: origin of the musculus obliquus inferior of arcus branchialis I in *Scomber* (LUBOSCH, 1938, p. 1019); intermediary attachment of the musculi transversi dorsales in Teleostei (LUBOSCH, 1938, p. 1023); origin of the musculus retractor arcuum branchialium dorsalis with its two portions (superior and inferior) in Teleostei; in a few Teleostei not only on the basioccipitale but also on the first vertebrae as in *Amia* (Lubosch, 1938, p. 1022).

Lateral wall of the skull: ventral of the origin of the musculus retractor hyomandibularis origin of the musculus levator arcus branchialis of arcus branchialis I in *Acipenser ruthenus* L. (Luther, 1938, p. 533); origin of fascicles of the musculus levator arcus branchialis of arcus branchialis IV in *Acipenser ruthenus* L. (Luther, 1938, pp. 533/534); laterally on a ridge of the skull, medial of the musculus adductor hyomandibularis, origin of the musculi levatores arcuum branchialium, a group of seven pairs of muscles, in *Amia* (Luther, 1938, p. 534).

Regio otica: on the sharp edge of the opisthoticum origin of the musculi levatores arcuum branchialium and moreover on the processus ascendens of the parasphenoid origin of a ventral head of the 1st musculus levator arcus branchialis in *Polypterus* (Luther, 1938, p. 534); on the ventral side of the labyrinth region origin of the musculi levatores arcuum branchialium of arcus branchialis I–IV in Dipneusta (Luther, 1938, p. 538); between petrosum and opisthoticum between the places of origin of the musculus adductor hyomandibularis and of the musculus adductor operculi origin of the musculi levatores arcuum branchialium in Teleostei; this origin can extend occipitalward as far as on the supraclaviculare (Luther, 1938, p. 532; Lubosch, 1938, p. 1018; see also Gregory, 1933, p. 438 for Apodes); the "subtemporal fossa", which lies on the lateral surface of the otic capsule, serves for the lodgment of the muscles which pull up the inferior pharyngeal bones in Cyprinoidei and in *Tarpon atlanticus* (C. & V.) (Gregory, 1933, pp. 141/142); on the lateral fossa of the cranium attachment of the powerful muscles, which draw the pharyngeal teeth on the ceratobranchialia V upward against the horny pad that rests on a bony projection from the basioccipitale, in Eventognathi and their allies (Gregory, 1933, p. 424).

Pteroticum: origin of the musculus trapezius profundus in Cyprinidae and in Cobitidae and Peturidae (Lubosch, 1938, p. 1019).

Processus postorbitalis: origin of the musculus trapezius profundus in Holocephali (Luther, 1938, p. 533).

Skull ventral of the orbita: origin of the two musculi levatores arcuum branchialium in *Callorhynchus* and in no other genus of the Selachii (Luther, 1938, p. 531).

Ceratohyale: attachment of the first musculus obliquus ventralis lateralis in Teleostei, it is lacking in Cobitidae and Acanthopterygii (Lubosch, 1938, p. 1021).

Hypohyale: attachment of the musculus pharyngo-arcualis in some Teleostei (Lubosch, 1938, p. 1021); attachment of some fibres of the musculus obliquus ventralis of arcus branchialis I in some Teleostei as in *Acipenser* (Lubosch, 1938, p. 1020).

Urohyale: attachment of the musculus pharyngo-arcualis in some Teleostei (Lubosch, 1938, p. 1021).

Branchial arches (without detailed indication): on the ventral part of the preceding arch insertion of the musculi interbranchiales of arcus branchialis I–IV in *Neoceratodus* (Luther, 1938, p. 538); on their ventral parts on the oral margins (as in Selachii; not on the caudal margins as in Chondrostei) attachment of the very feebly developed musculi constrictores dorsoventrales in Teleostei (Lubosch, 1938, p. 1017); on them for the greater part insertion of the musculi levatores arcuum branchialium in ganoids (LUTHER, 1938, p. 533); on arcus branchialis V insertion of the modified musculus adductor in Holocephali (LUTHER, 1938, p. 533); on the branchial arch belonging to the metamere in question and on the branchial arch in front of it origin and insertion of the musculus subarcualis rectus in ganoids (LUTHER, 1938, p. 537); on all branchial arches in Cyprinidae, generally on arcus branchialis IV and V as in *Acipenser* attachment of the musculi transversi ventrales (LUBOSCH, 1938, pp. 1020/1021).

Pharyngobranchialia: on their ventral margins from arcus branchialis I to III origin of the musculi interbranchiales in Holocephali (LUTHER, 1938, p. 532); to the dorsal surface of the pharyngobranchiale II and to the united pharyngobranchialia III, IV and V insertion of the musculus levator arcuum branchialium posterior in *Callorhynchus* (LUTHER, 1938, pp. 531/532); on the pharyngobranchiale II insertion of one portion and origin of the second portion of the musculus levator arcus branchialis of arcus branchialis II in *Acipenser ruthenus* L. (LUTHER, 1938, p. 533); on the caudal side of the pharyngobranchiale II partial origin of the strongest portion of the musculus levator arcus branchialis of arcus branchialis III in *Acipenser ruthenus* L. (LUTHER, 1938, p. 533); on the pharyngobranchiale I partial insertion of the musculus levator arcus branchialis of arcus branchialis I in *Polypterus* (LUTHER, 1938, p. 534); on the proximal end of pharyngobranchiale II attachment of the musculi levatores arcuum branchialium interni anterior and posterior in *Amia* (LUTHER, 1938, p. 534); on the pharyngobranchialia II and III insertion of the musculi levatores arcuum branchialium interni of the first two branchial arches in lower Teleostei (LUBOSCH, 1938, p. 1018); on the pharyngobranchialia of the following arches sometimes insertion of the musculi levatores arcuum branchialium externi in Teleostei, in which there are generally four musculi levatores externi in lower Teleostei, three in *Esox* and in Siluridae (LUBOSCH, 1938, p. 1018); on the pharyngobranchiale IV + V, dorsal of the horizontal ligament which connects the epibranchialia, origin of the modified musculus adductor in Holocephali (LUTHER, 1938, p. 533); on the dorsolateral side of the pharyngobranchiale I origin of the musculus arcualis dorsalis, caput anterius, in Squaliformes; on the dorsal end of the rostral margin of the pharyngobranchiale II origin of the musculus arcualis dorsalis, caput posterius, which fuses with the caput anterius towards the insertion; entirely similar musculi arcuales dorsales are found on the branchial arches II and III in pentanch sharks, on the branchial arches II to V in heptanch sharks; in many Squaliformes (*Squalus acanthias* L., *Somniosus*) the musculus arcualis dorsalis 4 is undivided due to the fusion of pharyngobranchiale IV and V; the same is the case with the musculus arcualis dorsalis 6 in *Heptanchus* (LUTHER, 1938, p. 528); the capita posteriora of the musculi arcuales dorsales are lacking in Batoidei (LUTHER, 1938, p. 531); on the mediocaudal side of the pharyngobranchiale I to III origin of the musculi arcuales dorsales of arcus branchialis I to III in Holocephali (LUTHER, 1938, p. 533); on the pharyngobranchialia attachment of the musculi obliqui dorsales mediales of the corresponding or of the next branchial arch in Teleostei; they are most constant on arcus branchialis III and IV, rare on arcus II, rudimentary on arcus I (*Scomber*) (LUBOSCH, 1938, p. 1018); on the caudal outer part of the last pharyngobranchiale for the greater part insertion of the musculus trapezius profundus in Holocephali

(Luther, 1938, p. 533); dorsally on pharyngobranchiale V origin of the musculus sphincter oesophagi in *Callorhynchus* (Luther, 1938, p. 539); on the pharyngobranchiale III origin of the three musculi obliqui dorsales in *Amia* (Luther, 1938, p. 540).

Epibranchialia: just at the place of the connection between epibranchiale and ceratobranchiale I and II insertion of the musculus levator arcuum branchialium anterior in *Callorhynchus* (Luther, 1938, p. 531); on the outer (dorsal) surface of the epibranchiale insertion of the musculus levator arcus branchialis of arcus branchialis I in *Acipenser ruthenus* L. (Luther, 1938, p. 533); on the epibranchiale II attachment of one of the two portions of the musculus levator arcus branchialis of arcus branchialis II in *Acipenser ruthenus* L. (Luther, 1938, p. 533); on the epibranchiale III insertion of the musculus levator arcus branchialis of arcus branchialis III in *Acipenser ruthenus* L. (Luther, 1938, p. 533); on the epibranchiale III partial origin of the musculus levator arcus branchialis of arcus branchialis IV in *Acipenser ruthenus* L. (Luther, 1938, pp. 533/534); on the epibranchiale I partial insertion of the musculus levator arcus branchialis of arcus branchialis I in *Polypterus* (Luther, 1938, p. 534); on the proximal part of the osseous epibranchiale I insertion of the musculus levator arcus branchialis externus 1 in *Amia* (Luther, 1938, p. 534); on the caudal margin of the cartilaginous epibranchiale II and III and on the osseous and cartilaginous epibranchiale IV partial insertion of the musculi levatores arcuum branchialium in *Amia* (Luther, 1938, p. 534); at the demarcation between the epi- and ceratobranchiale I–IV on these elements insertion of the musculi levatores arcuum branchialium of arcus branchialis I to IV in Dipneusta (Luther, 1938, p. 538); on the dorsocaudal side of epibranchiale I insertion of the musculus arcualis dorsalis, caput anterius, in Squaliformes (Luther, 1938, p. 528); on the caudal margin of the epibranchialia I to III, just above their connection with the ceratobranchialia, insertion of the musculi arcuales dorsales of arcus branchialis I to III in Holocephali (Luther, 1938, p. 533); on the epibranchialia the typical insertion of the musculi levatores arcuum branchialium in Teleostei (Lubosch, 1938, p. 1018); in grooves on the epibranchialia origin or insertion of the musculi adductores arcuum branchialium in Squaliformes (Luther, 1938, pp. 527, 530); from epibranchialia I to IV origin of the musculi adductores arcuum branchialium in *Chimaera*; this place of origin lies ventral of the horizontal ligament which connects the epibranchialia (Luther, 1938, p. 533); in shallow grooves of the epibranchialia of arcus branchialis I to III in *Acipenser sturio* L. and of arcus branchialis IV in *Acipenser ruthenus* L. and *fulvescens* Raf. origin of the musculi adductores arcuum branchialium (Luther, 1938, pp. 534/535); on the mediocaudal side of the epibranchiale of arcus branchialis I to IV origin of the musculi adductores arcuum branchialium in *Polyodon* (Luther, 1938, pp. 534/535); on the epibranchiale IV origin of the musculus adductor arcus branchialis IV and V in *Amia* (Luther, 1938, pp. 534/535); on the epibranchialia origin of the musculi adductores arcuum in Teleostei, among which only those of arcus branchialis IV are constant, and those of arcus branchialis V are often present (Lubosch, 1938, p. 1018); on the epibranchialia attachment of the musculi obliqui dorsales mediales of the corresponding or of the next branchial arch in Teleostei; they are most constant on arcus branchialis III and IV, rare on arcus II, rudimentary on arcus I

(*Scomber*) (Lubosch, 1938, p. 1018); on the epibranchialia of two consecutive arches attachment of the musculi obliqui inferiores in Teleostei (as a rule three, in *Scomber* five) (Lubosch, 1938, pp. 1018/1019); on the epibranchiale IV insertion of the first musculus obliquus dorsalis in *Amia* (Luther, 1938, p. 540).

Ceratobranchialia: on the ceratobranchialia II–IV insertion of the musculi levatores arcuum branchialium of arcus branchialis II–IV in *Polypterus* (Luther, 1938, p. 534); in grooves on the ceratobranchialia insertion or origin of the musculi adductores arcuum branchialium in Squaliformes (Luther, 1938, pp. 527, 530); on the dorsal part of the ceratobranchiale I–IV insertion of the musculi adductores arcuum branchialium in *Chimaera* (Luther, 1938, p. 533); in shallow grooves of the ceratobranchialia of arcus branchialis I–III in *Acipenser sturio* L. and of arcus branchailis IV in *Acipenser ruthenus* L. and *fulvescens* Raf. insertion of the musculi adductores arcuum branchialium (Luther, 1938, pp. 534/535); on the laterorostral side of the ceratobranchialia of arcus branchialis I–IV insertion of the musculi adductores arcuum branchialium in *Polyodon* (Luther, 1938, pp. 534/535); on the ceratobranchialia IV and V insertion of the musculi adductores arcuum branchialium of arcus branchialis IV and V in *Amia* (Luther, 1938, pp. 534/535); on the ceratobranchialia insertion of the musculi adductores arcuum in Teleostei, in which only those of arcus branchialis IV are constant and those of arcus branchialis V are often present (Lubosch, 1938, p. 1018); on the ceratobranchiale V origin of the musculus obliquus inferior 5 in *Scomber* (this muscle inserts on epibranchiale IV) (Lubosch, 1938, p. 1019); on the ceratobranchiale V insertion of the musculus trapezius profundus in Cyprinidae and in Cobitidae and Siluridae (Lubosch, 1938, p. 1019); on the ceratobranchialia I–IV attachment of the musculi obliqui ventrales in Teleostei (Lubosch, 1938, p. 1020); on the ceratobranchialia I–IV attachment of the musculi obliqui ventrales laterales in most Teleostei; they are lacking in Cobitidae and in Acanthopterygii (Lubosch, 1938, p. 1021); on the top of ceratobranchiale V attachment of the musculus pharyngo-arcualis in Teleostei (Lubosch, 1938, p. 1021); on the ceratobranchiale V insertion of the musculus obliquus dorsalis 2 in *Amia* (Luther, 1938, p. 540); on the dorsal top of the ceratobranchiale V insertion of the musculus retractor arcuum branchialium dorsalis superior and on its ventrocaudal surface insertion of the musculus retractor arcuum branchialium dorsalis inferior in Teleostei (Lubosch, 1938, p. 1022).

Hypobranchialia: from arcus branchialis I to III insertion of the musculi interbranchiales in Holocephali (Luther, 1938, p. 532); on the hypobranchialia partial attachment of the musculus obliquus ventralis in ganoids (Luther, 1938, p. 538); on the hypobranchialia I–IV attachment of the musculi obliqui ventrales of the corresponding arch in Teleostei, on the hypobranchiale III also partial attachment of the same muscle of arcus IV (Lubosch, 1938, p. 1020); on the hypobranchialia in front of the 5th attachment of the musculus pharyngo-arcualis in some Teleostei (Lubosch, 1938, p. 1021).

Basibranchiale: on the basibranchialia partial attachment of the musculus obliquus ventralis in ganoids (Luther, 1938, p. 538); on basibranchiale V partial insertion of the musculus sphincter oesophagi in *Callorhynchus* (Luther, 1938, p. 539).

Extrabranchialia superiora and inferiora: partial origin and insertion of the musculus interbranchialis in Squalidae (Spinacidae) and Carcharhinidae (LUTHER, 1938, p. 527).

48. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS TRIGEMINUS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

a. Introduction

On the one hand the attachment of the muscles that can move a mobile primary upper jaw are dealt with here, and on the other hand that of the muscles moving the lower jaw.

A mobile primary upper jaw occurs in a number of Sauropsida, *viz.* in those with a kinetic skull.

As regards the muscles of the lower jaw in Amphibia and Amniota, something must be said in this introduction about the principal places of origin of the jaw muscles. They are: the fossa temporalis, the margins of the fenestrae temporales, the zygomatic arches and, finally, the outer surface of the cerebral skull which, in connection with the attachment of the chewing-muscles, may bear a sagittal crest on the parietale and sometimes a crest on the occipitale (VERSLUYS, 1936, pp. 717, 718, 719, 720). In some cases accessory places of attachment for the origin of the jaw muscles occur by the side of these.

The fossa temporalis and the margins of the fenestrae temporales

Their importance as places of attachment for the chewing-muscles depends partly on the width and the shape of the fossae temporales, which must consequently be discussed.

In those animals which live in the water, where weight and girth of the head are not so important, we may – and in this connection we think especially of Reptilia – expect a wide fossa temporalis without lateral fenestrae temporales. In land animals, where weight and girth of the head play an important part, we see that a narrowing of the fossa temporalis occurs, connected with, and as a result of the narrowing of the skull. Here lateral fenestrae temporales occur, attended with a sometimes very far advanced reduction of the covering of the temporal region, and the disappearance of those spots that have no importance for the firmness of the skull. Through this reduction of the temporal region the chewing-muscles, situated in the narrowed fossa temporalis, have more room (MARINELLI, 1933, pp. 201/202; VERSLUYS, 1936, p. 718).

Mention may be made of the opinion that the enormous development of the chewing-musculature might be the cause of the lack of the postorbital bar in many Mammalia (STADTMÜLLER, 1936, p. 931).

The shape of the fossa temporalis is connected with the size and shape of the musculus temporalis. Synapsid †Theromorpha, with a relatively short snout, have an elongated and shallow fossa temporalis, supplied with a lateral fenestra temporalis. Diapsid and parapsid Reptilia, and †Ichthyosauria, with a relatively long snout, have a short, high fossa temporalis, supplied with a far dorsally situated fenestra temporalis (VERSLUYS, 1936, p. 719).

In fish eating Loricata, with a long and narrow snout, the musculus temporalis and the upper fenestra temporalis are larger than in the other Loricata (VERSLUYS, 1936, pp. 718, 789).

In Chamaeleonidae with their very short skulls the necessary space in the fossa temporalis for the chewing-muscles is obtained by a helmet-shaped upward increase of the very short temporal region (VERSLUYS, 1936, p. 779).

Temporal and zygomatic arches

Temporal and zygomatic arches play a very important part in the origin of the chewing-muscles, but by the side of that they also have a function in the suspension of the upper jaw and that of the jaw joint. It is, however, impossible to separate the share of each function in the construction of the temporal or zygomatic arches. Moreover, the structure of the zygomatic arch system is very intricate in itself.

MARINELLI has given a very interesting and stimulating dissertation on the temporal or zygomatic arch system (MARINELLI, 1929, pp. 129, 132, 133; 1933, pp. 203, 204, 219/220, 221, 222). From this we derive the following. According to him the temporal or zygomatic arch system may be compared to the central supporting part of a bridge construction, of which the columns are formed by the suspension of the jaw joint and the attachment of the new upper jaw. The load of this "bridge construction" is formed by the chewing-muscles attached to the temporal or zygomatic arches. The pressure exercised on the temporal or zygomatic arches is propagated through the entire bridge construction, not only from the point of application *via* the jaw joint and the back-teeth to the second point of application, but throughout the entire skull. Just as the arches or joists of a bridge are built as a grating to prevent deflection, the temporal or zygomatic arches are constructed in the same way. Not only the arches construction as a whole, but also its separate parts each have their own importance as constructive elements in the whole. From the shape and position of each joist and arch, its function may be derived. According to MARINELLI this is the positive factor of the origin of the broken secondary skull roof from its closed condition. In this transition the secondary skull roof no longer had the character of a primitive armour with a primary mosaic pattern, but the composing bones had already an individual character. It is possible that fenestrae occurred – in order to save material and weight, and to save space for the chewing-muscles – the skeleton remained where the functions demanded this, and this skeleton developed in such a way that the temporal or zygomatic arch system as a whole, but also in all its separate parts, was adapted as regards shape and strength to the functional demands made on it.

Outer surface of the cerebral skull

Chewing-muscles may also have their origin on the outer surface of the cerebral skull. This is the case in the attachment of the chewing-muscles in the fossa temporalis which we discussed above. Under this heading we shall only discuss those cases where the chewing-muscles find their origin on the outer surface of a cerebral skull the fossa temporalis of which is uncovered, such as occurs in Amphibia, †Cynodontia, Aves and Mammalia.

In connection with these attachments of muscles the outer surface of the cerebral skull may bear crests *etc.*

Accessory places of attachment

Apart from the places of attachment of the chewing-muscles mentioned above, others are found here and there.

In †Ceratopsia the helmet-like formation, which is a forerunner of the large neck shield, is perhaps only of importance because it made possible an elongation of the musculus temporalis (VERSLUYS, 1936, pp. 796/797).

b. The size

As regards the muscles of the lower jaw, the size and development of the place of origin of the jaw muscles is connected with the size of the jaw muscles, and this latter is connected with the size of the lower jaw; the size of the lower jaw depends on the size of the animal (STADTMÜLLER, 1936, pp. 951/952). It also depends on the character of the food so that the food in its turn influences the part the jaws play in the seizing, holding and chopping up of the food (MARINELLI, 1933, pp. 201–203; VERSLUYS, 1936, p. 719).

Discussing the musculus adductor mandibulae in Sauropsida, LUBOSCH (1938, pp. 1033/1034) says that one cannot help the impression that the musculature possesses an individual growth and development and constitutes an independent factor for the differentiation of the skull in addition to other factors as dentition, feeding, eyes, brain.

Temporal and zygomatic arches

We shall now discuss the data on the development of the temporal and zygomatic arches although this development is not directly connected with the size of the places of attachment of muscles on the temporal and zygomatic arches. Actually it is the size of these places of attachment which is of importance for our purpose.

In Amphibia

The weakly developed temporal arches play in Amphibia an unimportant part in the attachment of the chewing-muscles. It is a curious fact that in certain higher Caudata a so-called upper temporal arch ("pseudo-temporal arch") is found, the cause of which may perhaps be found in the exceptional greed of these animals and the stronger chewing-musculature connected with this (STADTMÜLLER, 1936, p. 613).

In Reptilia

High demands are made on the temporal arches of Reptilia where the old upper jaw in the kinetic skull is moved by a muscle inserted on the quadratum, as occurs in certain beasts of prey among Archosauria. In a second group of Reptilia where the old upper jaw is moved by a muscle inserted on the pterygoid to which belong Sauria and Serpentes, which eat insects or small animals and in doing so exert slight chewing-pressure, no high demands are made on the temporal arches; lower and sometimes also upper temporal arch are lacking in these animals (Versluys, 1936, pp. 720, 748/749, 775/776, 782). In Sauria the musculus temporalis is much more strongly developed than the musculi pterygoidei; the temporal region possesses an upper fenestra temporalis (Versluys, 1936, p. 719). According to Marinelli (1929, p. 135) the lateral chewing-muscles in *Varanus* pull almost at right angles on the upper temporal arch.

In durophages and beasts of prey among Reptilia whose prey is large (†Theromorpha, Loricata, *Sphenodon*) which, in connection with their food exert a great chewing-pressure, the temporal arches are strongly developed, while there is at the same time a postorbital arch (Versluys, 1936, p. 720).

In herbivorous Reptilia the temporal region may have been reduced but this need not be the case. The temporal region may *viz.* be used as an armour (*Chelonia*) (Versluys, 1936, pp. 721, 722).

In Aves

In Aves the weakly developed temporal arch does not play an important part in the attachment of the chewing-muscles.

In Mammalia

In Mammalia there is a direct connection between height and strength of the zygomatic arch and the strength of the muscles finding their origin there (*i.e.* the musculus masseter entirely or partly and part of the musculus temporalis) (Marinelli, 1933, p. 204; Stadtmüller, 1936, p. 931).

In Carnivora the development of the zygomatic arch is extreme in connection with the great development of the musculus masseter (Marinelli, 1933, p. 204). Opposite Carnivora with their strongly developed zygomatic arch can be placed Cetacea with their weakly developed zygomatic arch, connected with the loss of the chewing-function, especially in Mystacoceti (Stadtmüller, 1936, p. 958; Böker, 1937, p. 52).

But also in Carnivora we find important differences between Felidae with strongly developed zygomatic arches and Pinnipedia with weakly developed zygomatic arches connected with weakly developed back-teeth (Marinelli, 1929, p. 136). In Carnivora with strongly developed scissor-like mechanism ("Brechschere") the zygomatic arch is wide so that the musculus masseter has a component directed towards the median, giving a support against the laterally directed pressure exercised on the scissor-like mechanism (MARINELLI, 1929, p. 136). In *Panthera leo* (L.) the slanting musculus masseter helps in absorbing the backward displacement of the lower jaw in chewing (MARINELLI, 1929, p. 138).

But the development of the zygomatic arch is not in itself an indication for the development of the chewing-muscles. Thus, in Ungulata, the zygomatic arch is more weakly developed than in Carnivora, in connection with the fact that the origin of the musculus masseter has been moved forward, from the zygomatic arch to the side of the maxillare (MARINELLI, 1933, pp. 204/205). In *Giraffa camelopardalis* (L.) the musculus masseter is still situated on the outside of the body of the jugale and shows perhaps a slight transgression on the maxillare (MARINELLI, 1933, pp. 206, 208). In *Equus caballus* L., on the contrary, the musculus masseter has a large surface and runs from the jaw joint as far as halfway the series of back-teeth; it has its origin on the lower side of the zygomatic arch but also on the crista masseterica situated on the side of the maxillare; the musculus masseter has been displaced forward, therefore it pulls obliquely dorsorostrally (the insertion on the enlarged angulus mandibulae works in the same direction) (MARINELLI, 1933, pp. 212, 213, 217). So the musculus masseter exercises a chewing-pressure on the back-teeth. In *Equus caballus* L. part of the musculus temporalis as well finds its origin on the processus zygomaticus of the squamosum immediately over the joint, and exercises pressure both on the joint and the upper jaw (MARINELLI, 1933, pp. 212, 213).

In Insectivora the reduction of the zygomatic arch is incomprehensible; it cannot be caused by the reduction of the dentition and the chewing-muscles (STADTMÜLLER, 1936, p. 969).

The very great extension of the jugale in *Cuniculus* (*Coelogenys*) has an entirely different cause; it serves to receive the cheek pouch (STADTMÜLLER, 1936, p. 973).

Outer surface of the cerebral skull

In many cases it is seen that the increase of the size of the place of origin of the jaw muscles is combined with an enlargement of the skull surface, which, according to STADTMÜLLER (1936, p. 952) must, in the first place be regarded as an adaptation to the necessity of the successful devouring of great masses of food within a relatively short time. The consequent incongruencies between the visceral skeleton and the cerebral skull are removed by an enlargement of the surface.

By the side of this it is of great importance for an insight in the size of the places of attachment to have some knowledge of the development of crests and ridges on the outer surface of the cerebral skull. We shall, however, see that this development is no direct measure for that of the jaw muscles.

In Reptilia

In †Cynodontia the musculus temporalis is inserted on the skull surface with the aid of a median crest formed by frontalia and parietalia, which points to a mammalian origin of the musculus temporalis (Versluys, 1936, p. 804). To this may be added that the position of the plane of origin of the musculus temporalis as well is in †Cynodontia different from that of other Reptilia; this modification is partly caused by the size of the cerebral capsule which also influences the place of the jaw joint. The modification of the origin of the musculus temporalis and in the position of the jaw joint are the cause of the modified structure of the lower jaw and the modified insertion of the chewing-muscles on the dentale (Versluys, 1936, pp. 752/753).

In Aves

Owing to the enlargement of the eye and of the brain in Aves, the musculus adductor mandibulae externus is crushed up in the narrow space between orbita, squamosum, quadratum, parietale and pterygopalatinum; a kind of competition for space leads to an enlargement on the outer surface of the squamosum (Lubosch, 1938, p. 1036).

In Aves with the type of skull with a curved or cracked longitudinal axis the grooves for the chewing-muscles never reach as far as the medial line of the crown, and the skull roof remains free of muscle attachments, whereas in the straight type of skull the muscles secondarily reach upward along the wall of the cerebral skull as far as the crista sagittalis (Marinelli, 1936, pp. 834, 836/837).

In Mammalia

In those Mammalia whose dentition and jaws are relatively very strongly developed, it may be expected that the planes of attachment for the origin of the chewing-muscles on the skull surface are strongly developed as well, and that a powerful crista sagittalis occurs on the parietalia (Stadtmüller, 1936, p. 923). Especially in larger animals we may expect a strong development of crests and ridges, but there are also big skulls with thin skull walls and without crests (Stadtmüller, 1936, p. 951).

Among Carnivora fissipedia there are forms with elongated snouts and a crista sagittalis which crest has developed in connection with the development of the musculus temporalis, whereas by the side of them there are shortsnouted forms without crista formation but which, in their turn, show great width of the zygomatic arch and a deep fossa temporalis. These things depend on the development of the musculus masseter, resp. the musculus temporalis (Stadtmüller, 1936, p. 975).

In the big carnivorous Marsupialia we find bony ridges and muscular impressions whereas the smaller herbivorous and insectivorous Marsupialia have a smooth skull surface (Owen, 1866 II, p. 335).

Furthermore cristae for chewing-muscles occur in Insectivora (Stadtmüller, 1936, p. 955), in Otariidae (p. 976), rarely in Notoungulata (p. 979); among Artiodactyla only in Tylopoda and Tragulidae (p. 979), sometimes in Mesaxonia (p. 981), and in †*Protocetus* (p. 986), in part of the Lemuroidea and in an other part not (p. 988) and, finally, in some few cases among Pongidae a crista sagittalis and a crista occipitalis occur, which two cristae also occur in the Mesaxonia mentioned (pp. 955/956, 991) [1]).

Marinelli (1933) made a minute examination of the origin of the musculus temporalis and the musculus pterygoideus on the outer surface of the cerebral skull in *Giraffa camelopardalis* (L.) and *Equus caballus* L. The main points will be discussed here because they will give us an insight in the sizes of the different places of attachment.

In *Giraffa camelopardalis* (L.) the musculus temporalis is the strongest of the three chewing-muscles, and relatively powerful judging from the size of the fossa temporalis; the muscular fascicles coming from dorsal must have dominated, for the crista occipitalis is little pronounced (Marinelli, 1933, pp. 208, 210).

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[1]) For the development of this crista in gibbons see: A. H. Schultz (1944), Amer. J. Phys. Anthrop., n.s., **2**, pp. 1–129, especially pp. 85–86. (Postwar addition in the manuscript)

In *Equus caballus* L. the musculus temporalis diminishes in strength compared to the musculus masseter and the musculus pterygoideus; the area of origin of the musculus temporalis reaches the sagittal line of the crown of the skull, and may burden the inner wall of the fossa temporalis across the back ridge of its plane of origin, *i.e.* across the crista occipitalis in the same way as is the case in *Giraffa camelopardalis* (L.) (Marinelli, 1933, p. 212).

According to Marinelli (1929, p. 136) the musculus pterygoideus generally affects the molars in the same way as the musculus masseter has a special function when a scissor-like mechanism occurs. – In *Giraffa camelopardalis* (L.) the musculus pterygoideus is not very strong, it should have little influence on the chewing-pressure, but it leads in the first place the movements of the lower jaw; the origin of the musculus pterygoideus lies on the inner buttress of the attachment of the new upper jaw but continues from the jaw joint as far as the origin of the musculus temporalis (Marinelli, 1933, pp. 207, 208, 211). – In *Equus caballus* L. the origin of the musculus pterygoideus also lies on the inner support of the attachment of the new upper jaw, that is in the row formed by palatinum – pterygoid process of the basisphenoid – alisphenoid canal – squamosum, so on the inner wall of the fossa temporalis (Marinelli, 1933, pp. 212, 213). In *Equus caballus* L. the musculus pterygoideus is about equally powerful as the musculus masseter and affects the back-teeth *via* the "inner buttress".

c. The position

In Amphibia

Lateral wall of the skull: oralward of the foramen for the passage outward of the nervus V origin of the musculus levator quadrati in Apoda (Lubosch, 1938, p. 1025); on the same place origin of the lateral muscle-tract of the dorsal portion of the musculus levator bulbi in some Salamandrinae with a mobile quadratum (*Hynobius*, *Salamandrella*) (Lubosch, 1938, pp. 1025, 1026); partial origin of the musculus adductor mandibulae internus pterygoideus in Amphibia (Lubosch, 1938, p. 1030); on the parasphenoid and adjoining parts of the lateral wall of the skull origin of two parts of the musculus adductor mandibulae in *Siren* (Lubosch, 1938, p. 1032); origin of the deeper fascicles of the musculus adductor mandibulae internus in Caudata (Lubosch, 1938, pp. 1031/1032).

Regio otica: on the prooticum partial origin of the musculus adductor mandibulae internus pterygoideus in all Salientia (Lubosch, 1938, p. 1033); on the prooticum partial origin of the musculus adductor mandibulae internus pterygoideus and of the musculus adductor posterior longus in larval Salientia

(LUBOSCH, 1938, p. 1033); on the prooticum partial origin of the musculus adductor mandibulae externus in Amphibia (LUBOSCH, 1938, p. 1031); on the prooticum and on the cartilaginous wall of the labyrinth partial origin of the musculus adductor mandibulae posterior in Amphibia (LUBOSCH, 1938, p. 1031); on the dorsal surface of the labyrinth region origin of the musculus adductor mandibulae posterior longus (LUBOSCH, 1938, p. 1033).

Anulus tympanicus: partial origin of the musculus adductor mandibulae externus in Salientia (*Rana*, *Bufo*); this muscle is lacking in *Hyla*, *Bombina* (*Bombinator*), *Pelobates* and Pipidae (Aglossa) (LUBOSCH, 1938, p. 1032).

Fossa temporalis: on its rostral part origin of the musculus adductor mandibulae internus temporalis in Amphibia (LUBOSCH, 1938, p. 1030).

Squamosum: on the processus zygomaticus squamosi partial origin of the musculus adductor mandibulae externus in Salientia (*Rana*, *Bufo*), this muscle is lacking in *Hyla*, *Bombina* (*Bombinator*), *Pelobates* and Pipidae (Aglossa) (LUBOSCH, 1938, p. 1032); on the processus zygomaticus squamosi origin of the musculus adductor mandibulae posterior subexternus in Salientia (LUBOSCH, 1938, p. 1032); on the squamosum partial origin of the musculus adductor mandibulae posterior articularis in Salientia (LUBOSCH, 1938, p. 1033).

Paraquadratum: partial origin of the musculus adductor mandibulae externus in Amphibia (LUBOSCH, 1938, p. 1031).

Temporal arch: on the so-called upper or pseudo-temporal arch attachment of jaw muscles in some higher Caudata (STADTMÜLLER, 1936, p. 613).

Parietale and frontale: partial origin of the musculus adductor mandibulae internus in Caudata (LUBOSCH, 1938, p. 1031); no origin of the musculus adductor mandibulae internus temporalis (pseudotemporalis) in most Salientia, except in *Bombina* (*Bombinator*), *Xenopus* (*Dactylethra*), *Bufo granulosus* Spix, *Ceratophrys* (LUBOSCH, 1938, p. 1033); partial origin of the musculus adductor mandibulae internus pterygoideus in all Salientia (LUBOSCH, 1938, p. 1033); on the parietale only partial origin of the musculus adductor mandibulae externus in Amphibia (LUBOSCH, 1938, p. 1031); on both partial origin of the musculus adductor mandibulae externus in Apoda (LUBOSCH, 1938, p. 1032).

Nasopraemaxillare: towards this bone extension of the origin of the musculus adductor mandibulae externus in Apoda (LUBOSCH, 1938, p. 1032).

Suprarostrale: partial insertion of the musculi adductores mandibulae internus pterygoideus and posteriores in larval Salientia (LUBOSCH, 1938, p. 1033).

Pterygoquadratum bar: partial origin of the musculus adductor mandibulae internus pterygoideus in Amphibia (LUBOSCH, 1938, p. 1030).

Quadratum: on the processus pterygoideus of the quadratum insertion of the musculus levator quadrati in Apoda (LUBOSCH, 1938, p. 1025); on the same place insertion of the lateral muscle-tract of the dorsal portion of the musculus levator bulbi in some Salamandrinae with a mobile quadratum (*Hynobius*, *Salamandrella*) (LUBOSCH, 1938, pp. 1025, 1026); on the processus ascendens quadrati partial origin of the musculus adductor mandibulae internus pterygoideus and of the musculus adductor mandibulae posterior longus in larval Salientia (LUBOSCH, 1938, p. 1033); rostralward on the articular region of the quadratum origin of the musculi adductores mandibulae posteriores subexternus, articularis and lateralis in larval Salientia (LUBOSCH, 1938, p. 1033); partial origin of the musculus adductor mandibulae externus in Amphibia (LUBOSCH, 1938, p. 1031); on the processus zygomaticus quadrati partial origin of the musculus adductor mandibulae in Apoda (LUBOSCH, 1938, p. 1032); partial origin of the musculus adductor mandibulae posterior in Amphibia (LUBOSCH, 1938, p. 1031); origin of the musculus adductor mandibulae posterior lateralis in Salientia (LUBOSCH, 1938, p. 1032); partial origin of the musculus adductor mandibulae posterior articularis in Salientia (LUBOSCH, 1938, p. 1033).

Lower jaw: towards the inner surface of the lower jaw (goniale) direction of the fibres of the inner layer of the musculus adductor mandibulae internus in *Ambystoma* (*Siredon*) (LUBOSCH, 1938, p. 1031); ventralward on the lower jaw displacement of the insertion of the musculus adductor mandibulae internus in Caudata (LUBOSCH, 1938, pp. 1031/1032); on the articulare insertion of the dorsal portion of the musculus adductor mandibulae internus in *Siren* (LUBOSCH, 1938, p. 1032); upon the lateral surface of the lower jaw transgression of the ventral portion of the musculus adductor mandibulae internus in *Siren* (LUBOSCH, 1938, p. 1032); on the articular part of the lower jaw insertion of the musculus adductor mandibulae internus pterygoideus in all Salientia (LUBOSCH, 1938, p. 1033); on the Meckelian cartilage partial insertion of the musculus adductor mandibulae internus pterygoideus and of the musculi adductores mandibulae posteriores in larval Salientia (LUBOSCH, 1938, p. 1033); on the coronoid, goniale and for a smaller part on the dentale insertion of the musculus adductor mandibulae externus in Amphibia (LUBOSCH, 1938, p. 1031); on the gonio-articulare insertion of the musculus adductor mandibulae externus in Apoda (LUBOSCH, 1938, p. 1032); on the lateral surface of the goniale and of the Meckelian cartilage insertion of the musculus adductor mandibulae externus in Salientia (*Rana*, *Bufo*); this muscle is lacking in *Hyla*, *Bombina* (*Bombinator*), *Pelobates* and Pipidae (Aglossa) (LUBOSCH, 1938, p. 1032); on the articulare insertion of the musculus adductor mandibulae posterior in Amphibia (LUBOSCH, 1938, p. 1031).

In Reptilia

Crista parotica: accessory origin of the musculus protractor pterygoidei in Sauria (LUBOSCH, 1938, p. 1027).

Ala prootica: partial origin of the musculus adductor mandibulae internus temporalis profundus in Sauria (LUBOSCH, 1938, p. 1034).

Prooticum: on its processus anterior inferior accessory origin of the musculus protractor pterygoidei in *Sphenodon* (LUBOSCH, 1938, p. 1027); partial origin of the musculus levator pterygoidei in Sauria; this muscle is lacking in *Chamaeleon* (LUBOSCH, 1938, p. 1027); on its corpus partial origin of the musculus adductor mandibulae externus profundus (3) in Sauropsida (LUBOSCH, 1938, p. 1034); partial origin of the simple musculus adductor mandibulae internus temporalis (pseudotemporalis) in Testudinides (LUBOSCH, 1938, p. 1034).

Basisphenoid: constant origin of the musculus protractor pterygoidei in all Sauropsida (LUBOSCH, 1938, p. 1027); origin of the musculus retractor pterygoidei and of the musculus retractor vomeris in Serpentes (LUBOSCH, 1938, p. 1029).

Alisphenoid: origin of the simple musculus adductor mandibulae internus temporalis (pseudotemporalis) in Loricata (LUBOSCH, 1938, p. 1034).

Rostrum sphenoidale: accessory origin of the musculus protractor pterygoidei in Serpentes (LUBOSCH, 1938, p. 1027).

Parasphenoid: accessory origin of the musculus protractor pterygoidei in Sauria and in Serpentes (LUBOSCH, 1938, p. 1027).

Temporal region: on the squamosum, postfrontale, supratemporale and quadratojugale partial origin of the musculus adductor mandibulae externus superficialis and medius (1, 2) in Sauropsida (LUBOSCH, 1938, p. 1034); on the upper temporal arch attachment of lateral jaw muscles in *Varanus* (MARINELLI, 1929, p. 135).

Fossa temporalis: in its deeper regions partial origin of the musculus adductor mandibulae externus profundus (3) in Sauropsida (LUBOSCH, 1938, p. 1034); in its rostral region lies the musculus adductor mandibulae internus temporalis (pseudotemporalis) in Sauropsida (LUBOSCH, 1938, p. 1034); on the inner side of covering bones of the skull roof origin of important parts of the musculus temporalis in †Cotylosauria (VERSLUYS, 1936, p. 718).

Jugale: partial attachment of the musculus adductor mandibulae internus pterygoideus in *Uromastix* (LUBOSCH, 1938, p. 1035).

Parietale: partial origin of the musculus levator pterygoidei in Sauria (LUBOSCH, 1938, p. 1027); on its lateral surface and on its perpendicular lamella origin of the musculus levator pterygoidei in Serpentes, this muscle is lacking in some Serpentes and in *Sphenodon* (LUBOSCH, 1938, p. 1027); partial origin of the musculus levator bulbi ventralis in most Sauria, this muscle is lacking only in cases where the mobility of the pterygoid is small or has been lost entirely, as in *Chamaeleon* and *Pygopus* (LUBOSCH, 1938, p. 1028); partial origin of the musculus adductor mandibulae externus superficialis and medius (1, 2) in Sauropsida; partial origin of the musculus adductor mandibulae externus profundus (3) in Sauropsida (LUBOSCH, 1938, p. 1034); origin of the simple musculus adductor mandibulae internus temporalis (pseudotemporalis) in Serpentes and partial origin in Testudinides (LUBOSCH, 1938, p. 1034); on the parietale and praefrontale origin of the musculus adductor mandibulae internus temporalis superficialis in Sauria; on the parietale partial origin of the musculus adductor mandibulae internus temporalis profundus in Sauria (LUBOSCH, 1938, p. 1034); on a medial crest formed by parietale and frontale attachment of the musculus temporalis in †Cynodontia (VERSLUYS, 1936, p. 804).

Cartilago sphenolateralis: attachment of the musculus sphenopterygo-quadratus in the development of all Sauropsida (LUBOSCH, 1938, p. 1027).

Orbita. partial origin of the simple musculus adductor mandibulae internus temporalis (pseudotemporalis) in Testudinides (LUBOSCH, 1938, p. 1034).

Orbitosphenoid: accessory origin of the musculus protractor pterygoidei in Sauria and in *Sphenodon* (LUBOSCH, 1938, p. 1027).

Vomer: partial insertion of the musculus retractor pterygoidei and of the musculus retractor vomeris in Serpentes (LUBOSCH, 1938, p. 1029).

Old upper jaw: on the cartilaginous palatoquadratum bar attachment of the musculus sphenopterygo-quadratus during the development of all Sauropsida (LUBOSCH, 1938, p. 1027); on the epipterygoid partial origin of the musculus levator pterygoidei in Sauria (LUBOSCH, 1938, p. 1027); on the quadratum attachment of caudal fascicles of the musculus protractor pterygoidei in Boidae (Lubosch, 1938, p. 1027); on the dorsal margin of the epipterygoid partial origin of the musculus levator bulbi ventralis in most Sauria (Lubosch, 1938, p. 1028); on the pterygoid partial insertion of the musculus levator bulbi ventralis in most Sauria (Lubosch, 1938, p. 1028); on the palatinum and pterygoid partial insertion of the musculus retractor pterygoidei and of the musculus retractor vomeris in Serpentes (Lubosch, 1938, p. 1029); on the quadratum partial origin of the musculus adductor mandibulae externus superficialis, medius and profundus (1, 2, 3) in Sauropsida (Lubosch, 1938, p. 1034); on the epipterygoid partial origin of the simple musculus adductor mandibulae internus temporalis (pseudotemporalis) in Testudinides (Lubosch, 1938, p. 1034); on the epipterygoid partial origin of the musculus adductor mandibulae internus temporalis profundus in Sauria (Lubosch, 1938, p. 1034); on the pterygopalatinum bar with rostralward extension as far as the palatinum origin of the simple musculus adductor mandibulae internus pterygoideus in *Sphenodon*, Sauria, Testudinides and Serpentes; on the transversum and on the lateral and caudal surface of the pterygoid origin of the musculus adductor mandibulae internus pterygoideus ventralis and dorsalis in Loricata, on the dorsal surface of the palatinum partial origin of the musculus adductor mandibulae internus pterygoideus dorsalis in Loricata (Lubosch, 1938, p. 1035); on the quadratum origin of the musculus adductor mandibulae posterior in Reptilia (Lubosch, 1938, p. 1035); on the quadratum partial attachment of the musculus adductor mandibulae internus pterygoideus in *Uromastix* (Lubosch, 1938, p. 1035); on the quadratum insertion of the muscle which moves the primary upper jaw in a part of the Reptilia, to which certain carnivores among the Archosauria belong; on the pterygoid and not on the quadratum insertion of this muscle in another part of the Reptilia, to which the Sauria and Serpentes belong (Versluys, 1936, pp. 720, 748/749, 775/776, 782).

Lower jaw: insertion of the musculus protractor quadrati in some Serpentes (Lubosch, 1938, p. 1027); on the processus glenoidalis of the lower jaw attachment of fascicles of the musculus protractor quadrati in *Calamaria*, *Bungarus* and *Pelamis* (Lubosch, 1938, pp. 1027/1028); on the supraangulare insertion of the musculus adductor mandibulae externus superficialis, medius and profundus (1, 2, 3) in Sauropsida; on the coronoid, angulare and dentale also partial insertion of the musculus adductor mandibulae externus superficialis in *Sphenodon*, Sauria and Testudinides (Lubosch, 1938, p. 1034); on the medial surface of the lower jaw insertion of the simple musculus adductor mandibulae internus temporalis (pseudotemporalis) in Serpentes, Testudinides and Loricata (Lubosch, 1938, p. 1034); on the entrance to the canalis primordialis insertion of the musculus adductor mandibulae internus temporalis profundus in Sauria (Lubosch, 1938, p. 1034); partly medially on the lower jaw (gonioarticulare, angulare), partly transgressing on the lateral surface insertion of the musculus adductor mandibulae internus pterygoideus ventralis and on the medial surface of the lower jaw that of the musculus adductor mandibulae internus pterygoideus dorsalis in Loricata (Lubosch, 1938, p. 1035); on the gonioarticulare and on the entrance to the canalis primordialis insertion of the musculus adductor mandibulae posterior in Reptilia (Lubosch, 1938, p. 1035); in the canalis primordialis, on the Meckelian cartilage and on the dentale attachment of the musculus intramandibularis in Loricata (Lubosch, 1938, p. 1036).

In Aves

Basis cranii: on the basisphenoid constant origin of the musculus protractor pterygoidei in all Sauropsida (Lubosch, 1938, p. 1027); insertion of fascicles of the musculus adductor mandibulae internus pterygoideus ventralis in Psittaci, *Casuarius* and *Ardea* (Lubosch, 1938, p. 1036).

Prooticum: accessory origin of the musculus protractor pterygoidei in Aves (Lubosch, 1938, p. 1027); on its corpus partial origin of the musculus adductor mandibulae externus profundus (3) in Sauropsida (Lubosch, 1938, p. 1034).

Alisphenoid: accessory origin of the musculus protractor pterygoidei in Aves (Lubosch, 1938, p. 1027); partial origin of the musculus adductor mandibulae externus profundus (3) in Aves (Lubosch, 1938, p. 1034); partial origin of the musculus adductor mandibulae internus temporalis superficialis in Aves (Lubosch, 1938, p. 1034); partial origin of the musculus adductor mandibulae internus temporalis profundus in Aves (Lubosch, 1938, p. 1034).

Fossa temporalis: in its deeper regions partial origin of the musculus adductor mandibulae externus profundus (3) in Sauropsida (Lubosch, 1938, p. 1034); in its rostral region lies the musculus adductor mandibulae internus temporalis (pseudotemporalis) in Sauropsida (Lubosch, 1938, p. 1034).

Temporal region: on the squamosum, postfrontale, parietale, supratemporale and quadratojugale partial origin of the musculus adductor mandibulae externus superficialis and medius (1, 2) in Sauropsida; on the parietale partial origin of the musculus adductor mandibulae externus profundus (3) in Sauropsida (Lubosch, 1938, p. 1034).

Postfrontale: partial origin of the musculus adductor mandibulae internus temporalis superficialis in Aves (Lubosch, 1938, p. 1034).

Cartilago sphenolateralis: attachment of the musculus sphenopterygoquadratus in the development of all Sauropsida (Lubosch, 1938, p. 1027).

Orbita: on its caudal wall partial origin of the musculus adductor mandibulae internus temporalis superficialis in Aves (Lubosch, 1938, p. 1034).

Processus postorbitalis: origin of a portion of the musculus adductor mandibulae externus in Aves (Lubosch, 1938, p. 1036).

Septum interorbitale: accessory origin of the musculus protractor pterygoidei in Aves (Lubosch, 1938, p. 1027).

Ethmoidal region: on the mesethmoid accessory origin of the musculus protractor pterygoidei in Aves (Lubosch, 1938, p. 1027); far oralwards on the ethmoidal region origin of two musculi adductores mandibulae interni temporales in *Aprosmictus* (Lubosch, 1938, p. 1036).

Maxillare: partial origin of the musculus adductor mandibulae internus pterygoideus ventralis and dorsalis in Aves (Lubosch, 1938, p. 1035).

Palatoquadratum bar: on this cartilaginous bar attachment of the musculus sphenopterygo-quadratus during the development of all Sauropsida (Lubosch, 1938, p. 1027); on the quadratum insertion of part of the musculus cranio-pterygoquadratus, the so-called musculus protractor quadrati in Aves (Lubosch, 1938, p. 1028); on the processus orbitalis of the quadratum insertion of the musculus orbitoquadratus which moves the primary upper jaw in Aves (Versluys, 1936, pp. 748/749); on the quadratum partial origin of the musculus adductor mandibulae externus superficialis, medius and profundus (1, 2, 3) in Sauropsida (Lubosch, 1938, p. 1034); on the quadratum partial origin of the musculus adductor mandibulae internus temporalis profundus in Aves (Lubosch, 1938, p. 1034); on the transversum and on the lateral and caudal surface of the pterygoid partial origin of the musculus adductor mandibulae internus pterygoideus ventralis and dorsalis in Aves (Lubosch, 1938, p. 1035); on the quadratum origin of the musculus adductor mandibulae posterior in Aves (Lubosch, 1938, p. 1035).

Lower jaw: on the supraangulare insertion of the musculus adductor mandibulae externus superficialis, medius and profundus (1, 2, 3) in Sauropsida (Lubosch, 1938, p. 1034); on the entrance to the canalis primordialis insertion of the musculus adductor mandibulae internus temporalis superficialis in Aves (Lubosch, 1938, p. 1034); on the entrance to the canalis primordialis, on the goniale, on the supraangulare and on the Meckelian cartilage insertion of the musculus adductor mandibulae internus temporalis profundus in Aves (Lubosch, 1938, p. 1034); partly medially on the lower jaw (gonioarticulare, angulare), partly transgressing on the lateral surface insertion of the musculus adductor mandibulae internus pterygoideus ventralis and on the medial surface of the lower jaw that of the musculus adductor mandibulae internus pterygoideus dorsalis in Aves (Lubosch, 1938, p. 1035); on the gonioarticulare and on the entrance to the canalis primordialis insertion of the musculus adductor mandibulae posterior in Aves (Lubosch, 1938, p. 1035); on the lower jaw insertion of a portion of the musculus adductor mandibulae externus in Aves (Lubosch, 1938, p. 1036); on the dentale insertion of two musculi adductores mandibulae interni temporales in *Aprosmictus* (Lubosch, 1938, p. 1036).

Urohyale: on the copula II (urohyale) attachment of the third layer of the musculus intermandibularis in Aves, this layer is lacking in a number of Aves (Lubosch, 1938, pp. 1040/1041).

Ceratobranchiale: on the ceratobranchiale I attachment of the third layer of the musculus intermandibularis in Aves; this layer is lacking in a number of Aves (Lubosch, 1938, pp. 1040/1041).

In Mammalia

Basis cranii: attachment of the musculus mylohyoideus in primitive Mammalia (Lubosch, 1938, pp. 1074/1075); on the basis cranii (for another group this is described as pterygoid and tympanicum on the same page) partial origin of the caudal portion of the musculus intermandibularis profundus *s.* musculus mylohyoideus in *Myrmecophaga* (Lubosch, 1938, p. 1076).

Lateral surface of the skull: origin of the middle head of the musculus temporalis in Monotremata (Lubosch, 1938, p. 1068).

Os occipitale: partial attachment of the musculus pterygoideus medius in *Delphinus* (Lubosch, 1938, p. 1072).

Tympanic region: insertion of the musculus masseter and of the musculus pterygoideus internus in Mammalia (Lubosch, 1938, p. 1065); on the bulla tympani attachment of the superficial layer of the musculus masseter in Marsupialia (Lubosch, 1938, p. 1071); on the bulla tympani partial attachment of the musculus pterygoideus medius in Cetacea and on the tympanicum in *Delphinus* (Lubosch, 1938, p. 1072); on the processus styloideus partial attachment of the musculus pterygoideus medius in Cetacea (LUBOSCH, 1938, p. 1072); from the fissura petrotympanica partial origin of the musculus pterygotympanicus in Monotremata and Edentata and in *Homo* nearly as often as on the pterygoid (LUBOSCH, 1938, p. 1073); from the fissura petrotympanica partial origin of the musculus pterygotympanicus in the young *Choloepus* (LUBOSCH, 1938, p. 1073); probably on the petrosum, caudal of the foramen ovale, origin of the musculus pterygotympanicus in *Ornithorhynchus* (LUBOSCH, 1938, p. 1073); in the immediate vicinity of the bulla tympani partial origin of the musculus tensor veli palatini in *Didelphys* (LUBOSCH, 1938, p. 1073); on the bulla tympani partial origin of the musculus tensor veli palatini in Marsupialia and Pinnipedia (LUBOSCH, 1938, p. 1073); on the cartilage of the tuba auditiva main origin of the musculus tensor veli palatini in *Dasyurus*; on the cartilage of the tuba auditiva origin of the musculus tensor veli palatini in Insectivora, Artiodactyla and in part of the Primates and on it partial origin of the musculus tensor veli palatini in Marsupialia and Pinnipedia (LUBOSCH, 1938, p. 1073); on the wall of the labyrinth origin of one head of the musculus tensor tympani in *Ornithorhynchus* (LUBOSCH, 1938, p. 1074); in the fossa muscularis major of the promontorium origin of the musculus tensor tympani in most Mammalia (LUBOSCH, 1938, p. 1074); on the tympanic region partial origin of the musculus mylohyoideus in Mammalia (LUBOSCH, 1938, p. 1075); this is especially mentioned for the Monotremata (LUBOSCH, 1938, p. 1076).

Canalis temporalis: herein lies the caudal head of the musculus temporalis in Monotremata (LUBOSCH, 1938, p. 1068).

Ala temporalis: origin of the musculus pterygoideus internus in Monotremata (LUBOSCH, 1938, p. 1066).

Alisphenoid: origin of the musculus temporalis anterior in many cases of its occurrence in Mammalia (LUBOSCH, 1938, p. 1069).

Squamosum: attachment of fascicles of the musculus pterygoideus externus (lateralis) in *Tachyglossus* (LUBOSCH, 1938, p. 1069); origin of the musculus detrahens mandibulae in *Ornithorhynchus* (LUBOSCH, 1938, p. 1070); on the sutura squamosomastoidea and on the ventral surface of the squamosum origin of the musculus detrahens mandibulae in *Tachyglossus* (LUBOSCH, 1938, p. 1070).

Zygomatic arch: partial origin of the musculus masseter as a rule in Mammalia (LUBOSCH, 1938, p. 1067; see also MARINELLI, 1929, pp. 136, 138; MARINELLI, 1933, p. 204; STADTMÜLLER, 1936, pp. 931, 958, 969; BÖKER, 1937, p. 52); partial origin of the musculus zygomatico-mandibularis in Mammalia, this muscle is only lacking in *Delphinus* (LUBOSCH, 1938, p. 1068); attachment of superficial fascicles of the musculus masseter in *Phoca* (LUBOSCH, 1938, pp. 1071/1072).

Orbita: from it comes the rostral head of the musculus temporalis in Monotremata (LUBOSCH, 1938, p. 1068).

Orbitosphenoid: origin of the musculus temporalis anterior in many cases of its occurrence in Mammalia (LUBOSCH, 1938, p. 1069).

Foramen infraorbitale: through it runs the musculus zygomatico-mandibularis in Hystricomorpha (LUBOSCH, 1938, p. 1071); partial attachment of the musculus masseter in many Rodentia (STADTMÜLLER, 1936, pp. 973/974).

Upper jaw: partial origin of the musculus masseter as a rule in Mammalia (Lubosch, 1938, p. 1067; see also Marinelli, 1933, pp. 204/205, 206, 208, 212, 213, 217); attachment of the musculus zygomatico-mandibularis in Hystricomorpha (Lubosch, 1938, p. 1071).

Pterygoid region: partial origin of the musculus mylohyoideus in Mammalia (Lubosch, 1938, p. 1075); this is especially mentioned for the Monotremata (Lubosch, 1938, p. 1076).

Pterygoid: origin of the musculus adductor mandibulae internus (medialis) in Mammalia, this muscle is lacking in Monotremata; as a rule this muscle has two layers, the lateral fibres come from the fossa pterygoidea, the medial fibres from the processus pterygoideus and from the palatinum (Lubosch, 1938, pp. 1070/1071); origin of the musculus tensor tympani and of the musculus tensor veli palatini in the ontogeny and phylogeny of Mammalia (Lubosch, 1938, p. 1072); between spina angularis and lamina lateralis of the processus pterygoideus lies generally the musculus pterygotympanicus in *Homo* (Lubosch, 1938, pp. 1072/1073); partial insertion of the musculus pterygotympanicus in *Ornithorhynchus* (Lubosch, 1938, p. 1073); insertion of the musculus pterygotympanicus in the young *Choloepus* (Lubosch, 1938, p. 1073); on the processus pterygoideus partial insertion of the musculus tensor veli palatini in Marsupialia, Insectivora, Pinnipedia. Perissodactyla and Primates (Lubosch, 1938, p. 1073).

Malleus: insertion of the musculus tensor tympani in *Ornithorhynchus* (Lubosch, 1938, p. 1074).

Lower jaw: insertion of the musculi adductores mandibulae externus and internus in Mammalia (Lubosch, 1938, p. 1065); on the Meckelian cartilage insertion of the different portions of the musculus adductor mandibulae in embryonic stages of *Ornithorhynchus*, *Tachyglossus* and *Dasyurus* and in neonate *Dasyurus* (Lubosch, 1938, p. 1065); on the dentale insertion of the musculus pterygoideus internus in Monotremata (Lubosch, 1938, p. 1066); on the collum and corpus mandibulae insertion of the musculus detrahens mandibulae in *Ornithorhynchus*, on the caudal margin of the processus condyloideus as far as the angulus mandibulae in *Tachyglossus* (Lubosch, 1938, p. 1070); on its medial surface insertion of the lateral fibres of the musculus adductor mandibulae internus (medialis) (Lubosch, 1938, p. 1071); insertion of the superficial layer of the musculus masseter in the Sciuromorpha (Lubosch, 1938, p. 1071); on the Meckelian cartilage insertion of the musculus tensor tympani and of the musculus tensor veli palatini in the ontogeny and phylogeny of Mammalia (Lubosch, 1938, p. 1072); on the dentale attachment of superficial fibres of the musculus mylohyoideus in Mammalia (Lubosch, 1938, p. 1075); partial origin of the musculus intermandibularis profundus *s.* musculus mylohyoideus in *Ornithorhynchus* and *Manis*, not in *Tachyglossus* (Lubosch, 1938, p. 1076); on its angle partial origin of the caudal portion of the musculus intermandibularis profundus *s.* musculus mylohyoideus in *Myrmecophaga* (Lubosch, 1938, p. 1076); attachment of the musculus mylohyoideus in *Orycteropus* (Lubosch, 1938, p. 1076); on its ventral surface at the level of the alveolar plate attachment of the musculus intermandibularis superficialis in *Ornithorhynchus* (Lubosch, 1938, p. 1077).

Tongue bone: partial attachment of the musculus mylohyoideus in the phylogeny of Mammalia (Lubosch, 1938, p. 1075); on the corpus hyoidei attachment of the musculus mylohyoideus in *Orycteropus* (Lubosch, 1938, p. 1076); on the tongue bone attachment of the musculus intermandibularis superficialis in *Ornithorhynchus* (Lubosch, 1938, p. 1077).

d. Homology and non-homology

We have seen that the place of origin of the chewing-muscles is rather divergent even in closely related forms. As a special cause we may mention the case when the chewing-muscles lie now in the fossa temporalis, below the temporal covering of the secondary skull roof, and now on the free skull surface in those cases when a covered fossa temporalis is lacking, even if this controversion has been bridged by assuming the occurrence of an inner lamella below the chewing-muscles in the fossa temporalis (Marinelli, 1936, p. 819).

49. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS FACIALIS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Regio otica: partial origin of the deeper cranial head of the musculus depressor mandibulae in Caudata (Lubosch, 1938, p. 1044).

Anulus tympanicus: partial origin of the cranial head of the musculus depressor mandibulae in adult Salientia (Lubosch, 1938, p. 1045).

Temporal region: on the parietale, squamosum and paraquadratum partial origin of the superficial cranial head of the musculus depressor mandibulae in Caudata (Lubosch, 1938, p. 1044); on the squamosum partial origin of the deeper cranial head of the musculus depressor mandibulae in Caudata (Lubosch, 1938, p. 1044); on the "tympanicum" partial origin of the cranial head of the musculus depressor mandibulae in adult Salientia (Lubosch, 1938, p. 1045).

Quadratum: attachment of the two caudal parts of the musculus levator hyoidei (the musculus orbitohyoideus and the musculus suspensoriohyoideus) in larval Salientia (Lubosch, 1938, p. 1046); origin of two of the three oral parts of the musculus levator hyoidei in larval Salientia; the musculus quadrato-angularis originates on the processus muscularis of the quadratum, the musculus suspensorio-angularis originates on the rostral end of the quadratum (Lubosch, 1938, p. 1046); origin of the musculus suspensorio-angularis after metamorphosis in Salientia, this muscle is lacking in adult Salientia (Lubosch, 1938, pp. 1046, 1047).

Lower jaw: on the Meckelian cartilage insertion of the three oral parts of the musculus levator hyoidei in larval Salientia (Lubosch, 1938, p. 1046); on the medial surface of the lower jaw insertion of the musculus suspensorio-angularis after metamorphosis in Salientia; this muscle is lacking in adult Salientia (Lubosch, 1938, p. 1047).

Arcus hyalis: on its rostral end insertion of the musculus branchiohyoideus in larval Caudata and in some adult Perennibranchiata (*Proteus*, *Siren*, *Necturus* (*Menobranchus*)) (Lubosch, 1938, p. 1045); attachment of the two caudal parts of the musculus levator hyoidei (the musculus orbitohyoideus and the musculus suspensoriohyoideus) in larval Salientia (Lubosch, 1938, p. 1046); lateralwards of the hyoquadratum joint origin of the musculus hyoangularis, one of the three oral parts of the musculus levator hyoidei in larval Salientia (Lubosch, 1938, p. 1046).

Ceratohyale: origin of an accessory head of the musculus depressor mandibulae in *Siren* (Lubosch, 1938, p. 1044).

Ceratobranchiale: on the ceratobranchiale I origin of an accessory head of the musculus depressor mandibulae in larval salamanders, *Necturus* (*Menobranchus*) and *Amphiuma* (Lubosch, 1938, p. 1044); on the ceratobranchiale I origin of the musculus branchiohyoideus in larval Caudata and in some adult Perennibranchiata (*Proteus*, *Siren*, *Necturus* (*Menobranchus*)) (Lubosch, 1938, p. 1045).

In Reptilia

Occipitale: origin of the musculus extracolumellaris in Loricata (Lubosch, 1938, p. 1050).

Processus paroticus: origin of the musculus extracolumellaris in Sauria; among Sauria this muscle only remains in *Gekko* (Lubosch, 1938, p. 1050).

Squamosum: origin of the musculus extracolumellaris in Loricata (Lubosch, 1938, p. 1050).

Quadratum: partial origin of the musculus constrictor colli oralis in Sauria and *Sphenodon* (Lubosch, 1938, p. 1048).

Lower jaw: partial origin of the musculus constrictor colli oralis in Sauria and *Sphenodon* (Lubosch, 1938, p. 1048); on its caudal part partial origin of the musculus constrictor colli oralis in Loricata (Lubosch, 1938, p. 1049).

Extracolumella: on its process which lies in the tympanic membrane, insertion of the musculus extracolumellaris in embryonic stages of Sauria and Loricata (Lubosch, 1938, p. 1050); among Sauria this muscle only remains in *Gekko* (Lubosch, 1938, p. 1050).

In Aves

Occipitale: origin of the musculus extracolumellaris in Aves (Lubosch, 1938, p. 1050).

Squamosum: origin of the musculus extracolumellaris in Aves (Lubosch, 1938, p. 1050).

Extracolumella: on its process which lies in the tympanic membrane, insertion of the musculus extracolumellaris in embryonic stages of Aves (Lubosch, 1938, p. 1050).

In Mammalia

Basis cranii: attachment of the musculus levator hyoidei *s.* musculus stapedius in young embryonic stages of Mammalia and attachment of the musculus mastostyloideus in adult Monotremata, Xenarthra, *Neomys* (*Crossopus*), *Elephas* and Ungulata (Lubosch, 1938, p. 1091).

Processus mastoideus: origin of the musculus mallei externus which is found in embryonic *Mustela nivalis* L. (Lubosch, 1938, p. 1091).

Maxillare: attachment of the musculus bucinator in Monotremata (Lubosch, 1938, p. 1080); insertion of a fascicle with the character of a musculus sphincter which adjoins the musculus buccinalis in *Ornithorhynchus* and also in *Tachyglossus* (Lubosch, 1938, p. 1080).

Lower jaw: attachment of the musculus bucinator in Monotremata (Lubosch, 1938, p. 1080).

Malleus: on the lateral side of the manubrium mallei insertion of the musculus mallei externus which is found in embryonic *Mustela nivalis* L. (Lubosch, 1938, pp. 1077, 1091).

Stapes: attachment of the musculus stapedius in Theria (Ditremata) (Lubosch, 1938, p. 1091).

Tongue bone: on its ventral parts origin of the musculus stylohyoideus in Mammalia, except in *Hystrix*, *Bathyergus*, *Mustela*, *Meles*, *Hyaena*, *Proteles*, *Erinaceus*, Chiroptera, *Galeopithecus* and *Saimiri* (*Chrysothrix*) (Lubosch, 1938, p. 1092).

Hyoid arch: on the hyoid region origin of a fascicle with the character of a musculus sphincter which adjoins the musculus buccinalis in *Ornithorhynchus* (Lubosch, 1938, p. 1080).

Stylohyale: attachment of the musculus levator hyoidei *s.* musculus stapedius in young embryonic stages of Mammalia and attachment of the musculus mastostyloideus in adult Monotremata, Xenarthra, *Neomys* (*Crossopus*), *Elephas* and Ungulata (Lubosch, 1938, p. 1091); insertion of the musculus stylohyoideus in Mammalia, except in *Hystrix*, *Bathyergus*, *Mustela*, *Meles*, *Hyaena*, *Proteles*, *Erinaceus*, Chiroptera, *Galeopithecus* and *Saimiri* (*Chrysothrix*) (Lubosch, 1938, p. 1092).

50. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS GLOSSOPHARYNGEUS AND THE NERVUS VAGUS IN AMPHIBIA, SAUROPSIDA AND MAMMALIA

The position

In Amphibia

Skull (without detailed indication): attachment of the four musculi constrictores arcuum in Pipidae (Aglossa) (Lubosch, 1938, p. 1055); partial origin of the musculi levatores arcuum in Caudata, Apoda and in larval Salientia (Lubosch, 1938, p. 1051); insertion of the musculus levator arcus 2 or 2 + 3 or 3 in Caudata, in case the musculus levator arcus 1 has disappeared (Lubosch, 1938, p. 1054).

Occiput: generally origin of the first of the four musculi levatores arcuum in Caudata (Lubosch, 1938, p. 1051).

Regio otica: on the processus capsulae auditivae attachment of the muscles which connect the branchial skeleton with the cerebral skull in *Xenopus laevis* Daud. (Stadtmüller, 1936, p. 531); on the petrosum origin of the four musculi petrohyoidei in a number of Salientia, *e.g.* *Rana* (Lubosch, 1938, pp. 1056, 1057).

Tongue bone: attachment of the four musculi petrohyoidei in metamorphosed Salientia (Lubosch, 1938, p. 1056); the second of the three caudal musculi petrohyoidei is lacking in *Bufo arenarum* Hensel, some Brachycephalinae and in most Microhylidae (Brevicipitidae) (Lubosch, 1938, p. 1057); on its processus posteromedialis origin of the musculus dilatator laryngis in Salientia after metamorphosis (Göppert, 1937, pp. 808, 819, 850); on the caudal end of its processus posteromedialis origin of a superficial part of the musculus dilatator laryngis in adult *Rana* (Göppert, 1937, p. 808); on its processus posteromedialis origin of a deeper part of the musculus dilatator laryngis in adult *Rana* (Göppert, 1937, p. 809); on the end of the osseous part of its processus posteromedialis origin of the musculus hyolaryngeus in Salientia (Göppert, 1937, p. 811); on its processus posteromedialis (thyreohyale) attachment of caudal fascicles of the only musculus petrohyoideus in adult *Pipa pipa* (L.) (*Pipa americana*) (Lubosch, 1938, p. 1057).

Hyoid arch: on the hypohyale and basihyale insertion of the musculus interarcualis ventralis rectus 1 in Caudata (Lubosch, 1938, p. 1053); on the hyoid arch attachment of the musculus interarcualis ventralis rectus 1 in adult *Siphonops*, which in larval stages possesses the musculi interarcuales ventrales recti 1, 2 and 3 (Lubosch, 1938, p. 1054); on a caudal process of its copula insertion of the musculus interarcualis ventralis obliquus in larval Salientia (Lubosch, 1938, p. 1056).

Hyale: attachment of two musculi interarcuales ventrales recti in Salientia; these muscles disappear at the end of the metamorphosis (Lubosch, 1938, pp. 1055/1056).

Arci branchiales: on the ventral end of the ceratobranchiale II attachment of the four musculi constrictores arcuum in Pipidae (Aglossa); on the arcus branchialis IV attachment of the undivided musculus constrictor arcus in Salientia phaneroglossa (Lubosch, 1938, p. 1055); on the first three branchial arches insertion of the musculi levatores arcuum in Caudata, Apoda and larval Salientia (Lubosch, 1938, p. 1051); the three first branchial arches are connected by the musculi interarcuales (interbranchiales) in larvae of *Rana* (Lubosch, 1938, p. 1051); two consecutive branchial arches of the same side, are connected by three musculi interarcuales dorsales, thus running from arch to arch, in young stages of larvae of *Rana esculenta* L. (Lubosch, 1938, pp. 1051, 1055); these muscles disappear very early (Lubosch, 1938, p. 1056); the epibranchialia of the same side are connected by musculi interarcuales ventrales recti in Caudata, Apoda and larval Salientia (Lubosch, 1938, p. 1051); on the ceratobranchiale I origin of the musculus interarcualis ventralis rectus 1 in Caudata (Lubosch, 1938, p. 1053); on the ceratobranchiale II accessory origin of the musculus interarcualis ventralis rectus 1 in *Menopoma* (Lubosch, 1938, p. 1053); on the ventral ends of the epibranchialia I–III origin of the musculi interarcuales ventrales recti 2, 3 and 4 in Caudata, these muscles are attached to the epibranchiale IV (Lubosch, 1938, p. 1053); *Amphiuma* and *Necturus* (*Menobranchus*) possess two, *Megalobatrachus* (*Cryptobranchus*) three musculi interarcuales ventrales recti (Lubosch, 1938, p. 1053); in metamorphosis of Caudata only the first musculus interarcualis ventralis rectus remains (Lubosch, 1938, p. 1053); on the arcus branchialis I attachment of the musculus interarcualis ventralis rectus 1 in adult *Siphonops* (Lubosch, 1938, p. 1054); between the ceratobranchiale IV and II lies one of the three musculi interarcuales ventrales recti in Salientia; on the processus muscularis of the ceratobranchiale II and often on the ceratobranchiale I attachment of two other musculi interarcuales ventrales recti in Salientia; these muscles disappear at the end of the metamorphosis in Salientia (LUBOSCH, 1938, pp. 1055/1056); on the processus muscularis of the ceratobranchiale II origin of the musculus interarcualis ventralis obliquus in larval Salientia, this muscle disappears at the beginning of the metamorphosis (LUBOSCH, 1938, p. 1056); on the dorsal segment of the arcus branchialis III origin of the main part of the musculus hyopharyngeus in *Necturus*, in which the arcus branchialis IV is lacking (GÖPPERT, 1937, p. 807); on the arcus branchialis IV, which later on fuses with no III, origin of the musculus dorsopharyngeus with the exception of the most caudal part of this muscle, in larval *Ichthyophis*; the oral marginal part of this muscle detaches itself as musculus dilatator laryngis (GÖPPERT, 1937, p. 808); on a part of the arcus branchialis IV insertion of the musculus dilatator laryngis in Apoda (GÖPPERT, 1937, p. 850).

Laryngotracheal skeleton (without detailed indication): insertion of the musculus hyolaryngeus in some Salientia; this muscle is lacking in *Bombina* (*Bombinator*) (GÖPPERT, 1937, p. 811).

Arytaenoid: attachment of the oral marginal part of the musculus dorsopharyngeus, which detaches itself as musculus dilatator laryngis in *Ichthyophis* (GÖPPERT, 1937, p. 808); on the margin of the arytaenoid which limits the entrance to the larynx partial insertion of a superficial part of the musculus dilatator laryngis in adult *Rana* (GÖPPERT, 1937, p. 808); on its margin insertion of a deep portion of the musculus dilatator laryngis in some Salientia; in a part of the Salientia this deep portion is divided into a pars hyocricoidea and a pars cricoarytaenoidea as a consequence of the attachment to the processus muscularis of the pars cricoidea; this differentiation is lacking in *Bufo*, *Alytes*, *Pelobates*, *Pipa* and other Salientia (GÖPPERT, 1937, pp. 808, 809); on its rostral end resp. its oral margin insertion of the musculus dilatator laryngis in Amphibia (GÖPPERT, 1937, p. 851).

Cartilago apicalis: partial insertion of a superficial part of the musculus dilatator laryngis in adult *Rana* (GÖPPERT, 1937, p. 808).

Cricoid: partial origin of the musculus dilatator laryngis in *Rana* (GÖPPERT, 1937, p. 850; see also pp. 808, 809, 819).

Trachea: insertion of part of the musculus hyopharyngeus in *Necturus* (GÖPPERT, 1937, p. 807).

In Reptilia

Lower jaw: insertion of the musculus branchiomandibularis (visceralis) in some Sauria (LUBOSCH, 1938, p. 1058); attachment of a prolongation of the musculus interarcualis ventralis rectus in *Iguana* (LUBOSCH, 1938, p. 1058); attachment of two musculi interarcuales in *Cadea* (*Amphisbaena*) (LUBOSCH, 1938, p. 1058); attachment of such a muscle in *Leiolepis* (LUBOSCH, 1938, p. 1058).

Arcus hyalis, arci branchiales and tongue bone: on the dorsal part of the cornu hyale attachment of separate portions of the musculus interarcualis ventralis rectus in *Varanus* (LUBOSCH, 1938, p. 1058); between the cornu hyale and the cornu branchiale I runs the musculus interarcualis ventralis rectus in Sauria (LUBOSCH, 1938, p. 1058); between the cornu hyale and the cornu branchiale lies an intercorneal muscle in Testudinides (Lubosch, 1938, p. 1058); on the ceratobranchiale I attachment of two musculi interarcuales in *Cadea* (*Amphisbaena*) (Lubosch, 1938, p. 1058); on the ceratobranchiale I attachment of such a muscle in *Leiolepis* with intermediate attachment on the ceratohyale (Lubosch, 1938, p. 1058); on the ceratobranchiale II origin of such a muscle in *Phrynosoma* (Lubosch, 1938, p. 1058); on the caudal horns of the tongue bone partial origin of the musculus dilatator laryngis in *Amphisbaena fuliginosa* L.; this is the most original situation in Reptilia (Göppert, 1937, pp. 819, 850); on the caudal part of the tongue bone origin of the musculus retractor laryngis in Serpentes (Göppert, 1937, p. 821).

Arytaenoid: along its entire length, only leaving free the top, insertion of the musculus dilatator laryngis *s.* musculus crico-arytaenoideus in some Serpentes, such as *Natrix natrix* L. (*Tropidonotus natrix*), which in this respect has retained the most original situation in Reptilia (Göppert, 1937, p. 820); on its top and on its basis insertion of the musculus dilatator laryngis in *Coronella austriaca* Laur. (*Coronella laevis*) and in *Cadea* (*Amphisbaena*) (Göppert, 1937, p. 820); on its oral part or margin insertion of the musculus dilatator laryngis in Reptilia in general, as f.i. in *Sphenodon*, *Crocodylus* and in *Chelonia* (Göppert, 1937, pp. 820, 851); on the processus muscularis on its outer side attachment of the musculus dilatator laryngis in some Testudinides (Göppert, 1937, p. 818); caudally on the broad arytaenoid origin of the musculus laryngeus dorsalis and partial origin of the musculus laryngeus ventralis in *Natrix* (*Tropidonotus*) (Göppert, 1937, p. 820).

Cricoid: origin of an important part of the musculus dilatator laryngis in *Amphisbaena fuliginosa* L. (Göppert, 1937, pp. 819, 850); entire origin of the musculus dilatator laryngis *s.* musculus crico-arytaenoideus in practically all Reptilia, partial origin in Serpentes (Göppert, 1937, pp. 815, 819); on a alteral processus origin of the musculus crico-arytaenoideus in *Sphenodon*, Gekkonidae (Ascalabotae) and *Gekko* (*Platydactylus*) (Göppert, 1937, pp. 815, 819/820); ventrally on its long cartilaginous processus cranialis medianus ventralis partial origin of the musculus laryngeus ventralis in *Natrix* (*Tropidonotus*) (Göppert, 1937, pp. 816, 820); on its processus cranialis medianus dorsalis insertion of part of the fibres of the musculus laryngeus dorsalis in *Natrix* (*Tropidonotus*) (Göppert, 1937, pp. 816, 820/821); on its side, immediately adjacent the place of origin of the musculus dilatator laryngis, insertion of the musculus retractor laryngis in Serpentes (Göppert, 1937, p. 821).

Trachea: on the first tracheal ring partial origin of the musculus crico-arytaenoideus in Serpentes (Göppert, 1937, p. 819).

In Aves

Arytaenoid: on its often broad lateral margin insertion of the oral parts of the closing musculature of the larynx, the so-called musculus crico-arytaenoideus lateralis, in Aves (Göppert, 1937, p. 829); on the margin of its ventral surface as far as the caudal border of the lateral incision of the cartilage insertion of the musculus crico-arytaenoideus lateralis in *Struthio camelus* L. (Göppert, 1937, p. 829); on the lateral margin of its rostral end insertion of the musculus crico-arytaenoideus dorsalis in Aves, similar to the musculus dilatator laryngis in Reptilia (Göppert, 1937, p. 829); on the lateral margin of its rostral broad part insertion of the musculus crico-arytaenoideus dorsalis in *Struthio camelus* L. (Göppert, 1937, p. 829).

Cricoid: on its ventral margin, more caudalwards on its outer side and finally on its dorsal surface partial origin of the closing musculature of the larynx in Aves (Göppert, 1937, pp. 828/829); on the ventral surface of its ventral rostral processus, continuing on its outer surface and as far as the dorsalward directed anular part origin of the musculus crico-arytaenoideus lateralis in *Struthio camelus* L. (Göppert, 1937, p. 829); on its caudal marginal part, lateral of the root of the procricoid, origin of the musculus crico-arytaenoideus dorsalis in Aves, similar to the musculus dilatator laryngis in Reptilia (Göppert, 1937, p. 829); on its dorsal surface origin of the musculus crico-arytaenoideus dorsalis in *Struthio camelus* L. (Göppert, 1937, p. 829).

In Mammalia

Stylohyale: origin of fascicles of the musculus stylopharyngicus, the so-called pars thyreoidea (lacking in *Erinaceus*, Carnivora and *Equus*) (Lubosch, 1938, p. 1096); attachment of two musculi subarcuales recti in *Tachyglossus* (Lubosch, 1938, p. 1099).

Branchial arches: between branchiale I and II, between I and III and bteween II and III run musculi subarcuales recti in *Tachyglossus* and partly in other Mammalia (Lubosch, 1938, p. 1099); on the branchiale I attachment of two musculi subarcuales recti in *Tachyglossus* (Lubosch, 1938, p. 1099); the two arci thyreoidei are connected by the musculus interthyreoideus in Monotremata; this muscle is lacking in all other Mammalia (Göppert, 1937, pp. 837, 855); on the ventral part of arcus thyreoideus II partial origin of the musculus dilatator laryngis, the so-called musculus cerato-crico-arytaenoideus in Monotremata (Göppert, 1937, pp. 849/850); on the dorsal side of the copula of the cartilago thyreoides and more caudally on the arcus thyreoideus II partial origin of the musculus thyreo-crico-arytaenoideus lateralis in Monotremata (Göppert, 1937, p. 851); on the arcus thyreoideus II insertion of the fibres on the dorsal margin only of the musculus thyreo-cricoideus in *Tachyglossus* (Göppert, 1937, pp. 855, 863).

Cartilago thyreoides: attachment of fascicles of the musculus stylopharyngicus, the so-called pars thyreoidea (lacking in *Erinaceus*, Carnivora and *Equus*) and of the musculus palatopharyngeus (Lubosch, 1938, p. 1096); on its cornu caudale partial origin of the musculus cerato-crico-arytaenoideus in Marsupialia (Göppert, 1937, p. 850); on its cornu partial origin of the musculus cerato-crico-arytaenoideus in Cetacea only among Eutheria (Placentalia) (Göppert, 1937, p. 850); on its cornu caudale origin of the musculus cerato-arytaenoideus which occurs as a variety in Pongidae and in *Homo* (Göppert, 1937, p. 850); on its inner side partial origin of the musculus thyreo-arytaenoideus lateralis in Eutheria (Placentalia) (Göppert, 1937, p. 853); on its upper margin origin of the musculus thyreo-arytaenoideus superior descendens, a very variable muscle in *Homo* (Göppert, 1937, p. 853); on its ventral margin and often on its inner surface insertion of the musculus cricothyreoideus in Eutheria (Placentalia) (Göppert, 1937, p. 855); on its inner surface often a strong transgression of the insertion of the so-called musculus cricothyreoideus internus in some Primates, such as *Lemur*, *Alouatta* (*Mycetes*), *Cebus*, *Papio* (*Cynocephalus*); on the ventral edge only of the inner surface of the lamina thyreoidea insertion of the unindependant pars interna of the musculus cricothyreoideus in Pongidae and in *Homo*; on its cornu caudale insertion of the pars obliqua of the musculus cricothyreoideus externus in *Homo* (Göppert, 1937, p. 855).

Arytaenoid: on its processus muscularis insertion of the musculus cerato-crico-arytaenoideus in Monotremata, as occurs in Mammalia in general with the musculus crico-arytaenoideus; in Eutheria (Placentalia) this insertion can also raise itself a little on a sharp edge rising from the processus muscularis on its outer side (Göppert, 1937, p. 850); its caudal part, the ventral end of its outer side and the processus muscularis, are the places of attachment of the muscle (Göppert, 1937, p. 851); in the same place of that of the insertion of the musculus crico-arytaenoideus insertion of the musculus cerato-arytaenoideus which occurs as a variety in Pongidae and in *Homo* (Göppert, 1937, p. 850); on its ventral side and especially on its lateral margin as far as the processus muscularis, insertion of the musculus thyreo-crico-arytaenoideus lateralis in Monotremata (Göppert, 1937, p. 851); on its lateral margin as far as the processus muscularis insertion of the musculus thyreo-crico-arytaenoideus lateralis in Marsupialia (Göppert, 1937, p. 852); on its processus muscularis insertion of the musculus crico-arytaenoideus lateralis in Eutheria (Placentalia) except in Odontoceti, where this muscle is lacking (Göppert, 1937, p. 853); adjoining the musculus crico-arytaenoideus lateralis, on its processus muscularis, on its crista muscularis and on its lateral surface insertion of the musculus thyreo-arytaenoideus lateralis in Eutheria (Placentalia) (Göppert, 1937, p. 853); on the arytaenoid attachment of a fascicle of the musculus thyreo-arytaenoideus in Ruminantia (Göppert, 1937, p. 853); on its processus muscularis attachment of the musculus thyreo-arytaenoideus superior descendens, a very variable muscle in *Homo* (Göppert, 1937, p. 853); on the arytaenoid, opposite the place of insertion of the musculus thyreo-crico-arytaenoideus lateralis, as far as the processus muscularis attachment of the musculus ary-proarytaenoideus in Monotremata (Göppert, 1937, p. 851); between the processus muscularis and the top of the opposite arytaenoid runs the musculus interarytaenoideus obliquus in *Homo* (Göppert, 1937, pp. 852/853).

Proarytaenoid: attachment of the musculus ary-proarytaenoideus in Monotremata, and partly in Marsupialia and in some Eutheria (Placentalia), such as in many Carnivora (Göppert, 1937, pp. 851, 852); on the proarytaenoid attachment of the musculus crico-proarytaenoideus in Monotremata and in Marsupialia, this muscle being markedly strongly developed in *Tachyglossus* and lacking in Eutheria (Placentalia) (Göppert, 1937, pp. 851, 852, 854).

Cricoid: on its lateral and ventral part partial origin of the musculus cerato-crico-arytaenoideus in Monotremata (Göppert, 1937, p. 850); on that part of the cricoid that is immediately connected with the cornu caudale of the cartilago thyreoides and on the ventral dorsal surface on the side of the median incisure partial origin of the musculus cerato-crico-arytaenoideus in Marsupialia (Göppert, 1937, p. 850); on the dorsal part of the cricoid of which the dorsal part had developed into a broad plate, the so-called lamina, entire origin of the musculus crico-arytaenoideus in the Eutheria (Placentalia) with the exception of the Cetacea; in these Eutheria (Placentalia) the lamina often bears a median crista dorsalis, which enlarges and separates the places of origin of right and left muscle (GÖPPERT, 1937, pp. 841, 850); on its lateral surface partial origin of the musculus thyreo-crico-arytaenoideus lateralis in Monotremata (GÖPPERT, 1937, p. 851); on the dorsal part of the bar of the cricoid origin of the musculus crico-arytaenoideus lateralis in Eutheria (Placentalia), except in Odontoceti, where that muscle is lacking (GÖPPERT, 1937, p. 853); on the cricoid attachment of the musculus crico-proarytaenoideus in Monotremata, on its dorsal side in Marsupialia; this muscle is markedly strongly developed in *Tachyglossus* and is lacking in Eutheria (Placentalia) (GÖPPERT, 1937, pp. 851, 852); on its outer side a little below and dorsal of the thyreocricoid connection origin of the musculus thyreocricoideus in *Tachyglossus*; this muscle occurs only in the Monotremata (GÖPPERT, 1937, pp. 854/855); on the arch of the cricoid origin of the musculus cricothyreoideus in Eutheria (Placentalia) (GÖPPERT, 1937, p. 855).

Cartilage of the epiglottis: on its base attachment of a fascicle of the musculus thyreoarytaenoideus in Ruminantia (GÖPPERT, 1937, p. 853).

51. PLACES OF ATTACHMENT OF THE MUSCULATURE, INNERVATED BY THE NERVUS HYPOGLOSSUS-CERVICALIS IN SAUROPSIDA AND IN MAMMALIA

The position

In Reptilia

Lower jaw: on its rostral part origin of the musculus protractor laryngis in Serpentes (GÖPPERT, 1937, p. 821); on the inner side of the "mandibula" origin of the musculus protractor laryngis in Chamaeleonidae (GÖPPERT, 1937, p. 823).

Cricoid: on the side of its processus cranialis medianus ventralis insertion of the musculus protractor laryngis in Chamaeleonidae (GÖPPERT, 1937, p. 823).

Trachea: on the side of the trachea, a little caudal of the place of insertion of the musculus dilatator laryngis, insertion of the musculus protractor laryngis in Serpentes (GÖPPERT, 1937, p. 821).

In Aves

Tongue bone: attachment of a third pair of muscles in Psittaci (STRESEMANN, 1937, p. 879).

Trachea: on a number of tracheal rings only attachment of the musculus trachealis in some Aves, such as *Gallus*, *Ophisthocomys*, *Larus*, Anseres and Sphenisci (STRESEMANN, 1937, p. 877); on tracheal rings and either on bronchial cartilages or on the membrana tympaniformis externa of the wall of the bronchi attachment of the musculus tracheobronchialis (STRESEMANN, 1937, p. 877); on the trachea, cranialwards of the skeletal syrinx ("Trommel") origin of the musculi tracheobronchiales *s.* laryngosyringei, on the upper range of the skeletal syrinx origin of the musculi syringei; the insertion of these two groups of the musculi tracheobronchiales lies partly on the three first bronchial cartilages (in the akromyodal condition insertion on the ends of the halfrings, in the mesomyodal condition on the lateral surfaces of the halfrings), partly on the vibrating membranes or on the framing cartilages of these membranes (STRESEMANN, 1937, pp. 878/879); between the last but two tracheal ring and the upper bronchial ring runs a long pair of muscles in Psittaci, in which the musculus sternotrachealis is lacking (STRESEMANN, 1937, p. 879); between the last but one or last tracheal ring and a pair of rods that lies cranialward of the upper unmodified bronchial ring runs a short pair of muscles in Psittaci (STRESEMANN, 1937, p. 879); on the upper bronchial cartilages attachment of a third pair of muscles in Psittaci (STRESEMANN, 1937, p. 879).

In Mammalia

Tongue bone: on its corpus entire or partial origin of the musculus hyo-epiglotticus in Eutheria (Placentalia); the origin of this muscle can transgress upon the beginning of its second horn; in other cases origin on its rostral horn (GÖPPERT, 1937, p. 856).

Cartilage of the epiglottis: on the lingual surface of its base insertion of the musculus hyo-epiglotticus in Eutheria (Placentalia) (GÖPPERT, 1937, p. 856).

52. CAVITY OR GROOVE CONTAINING ELECTRIC ORGANS

a. The size

Judging from the picture in HOLMGREN & STENSIÖ (1936, fig. 211), the imprints caused by the electric organs upon the skull of † Cephalaspidae, may be called relatively large.

In *Astroscopus y-graecum* (C.V.) the vacuities which accomodate those parts of the eye muscles which are greatly hypertrophied and modified into powerful electric organs, are called very large and are said to fill a great space (GREGORY, 1933, pp. 367/368, 439, figs 247, 248; BALLOWITZ, 1938, p. 672) (see my figs 42, 50).

b. The position

In † Cephalaspidae the imprints of the electric organs upon the skull are situated on the dorsal side (HOLMGREN & STENSIÖ, 1936, fig. 211).

In *Astroscopus y-graecum* (C.V.) the situation of the vacuities for the electric organs is postorbital, they extend from the skin of the crown of the head unto the roof of the mouth cavity and are confluent with the orbitae (GREGORY, 1933, pp. 367/368, 439, figs 247, 248; BALLOWITZ, 1938, p. 672) (see my figs 42, 50).

c. Homology and non-homology

The difference in position might perhaps be explained by non-homology of the electric organs in the cases just mentioned.

The derivation of the electric organs in the † Cephalaspidae is unknown to me.

In *Astroscopus y-graecum* (C.V.) they are hypertrophied and modified eye muscles; with the dorsal shifting of the eye muscles and their derivatives, the primitive eye-muscle canal beneath the floor of the brain case has been abandoned and the myodome on the base of the skull has been closed up (Gregory, 1933, pp. 367/368, 439).

53. FORAMEN OCCIPITALE

a. The size

Here, as in previous sections, absolute and relative size will be treated separately.

The absolute size

Exact data concerning the absolute size of the foramen occipitale are not mentioned in the literature consulted ¹).

The absolute size of the foramen occipitale can be very different indeed. It is connected with the size of the cross section at the transition of the myelencephalon into the medulla spinalis, which depends upon the size of the animal. The bigger the animal the larger the foramen occipitale, generally speaking, will be. Sometimes other factors play a part. Marinelli (1936, p. 820) *e.g.* mentions that in Aves the size of the foramen occipitale is not determined by the inclination of the planum occipitale, but by the auditory capsules.

The relative size

The relative size of the foramen occipitale also can be rather different (see my fig. 159). For the greater part these differences will depend upon the differences in the size of the cross section at the transition of the myelencephalon into the medulla spinalis. For on the authority of the investigations of Dubois we may assume that among closely related, homoneurous species the cross section at the transition of the myelencephalon into the medulla spinalis will be relatively larger in the smaller species

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¹) See: C. E. Keeler (1941). Hereditary shape differences in the foramen magnum of inbred rats. Genetics, **26**, pp. 157—158. (Postwar addition in the manuscript)

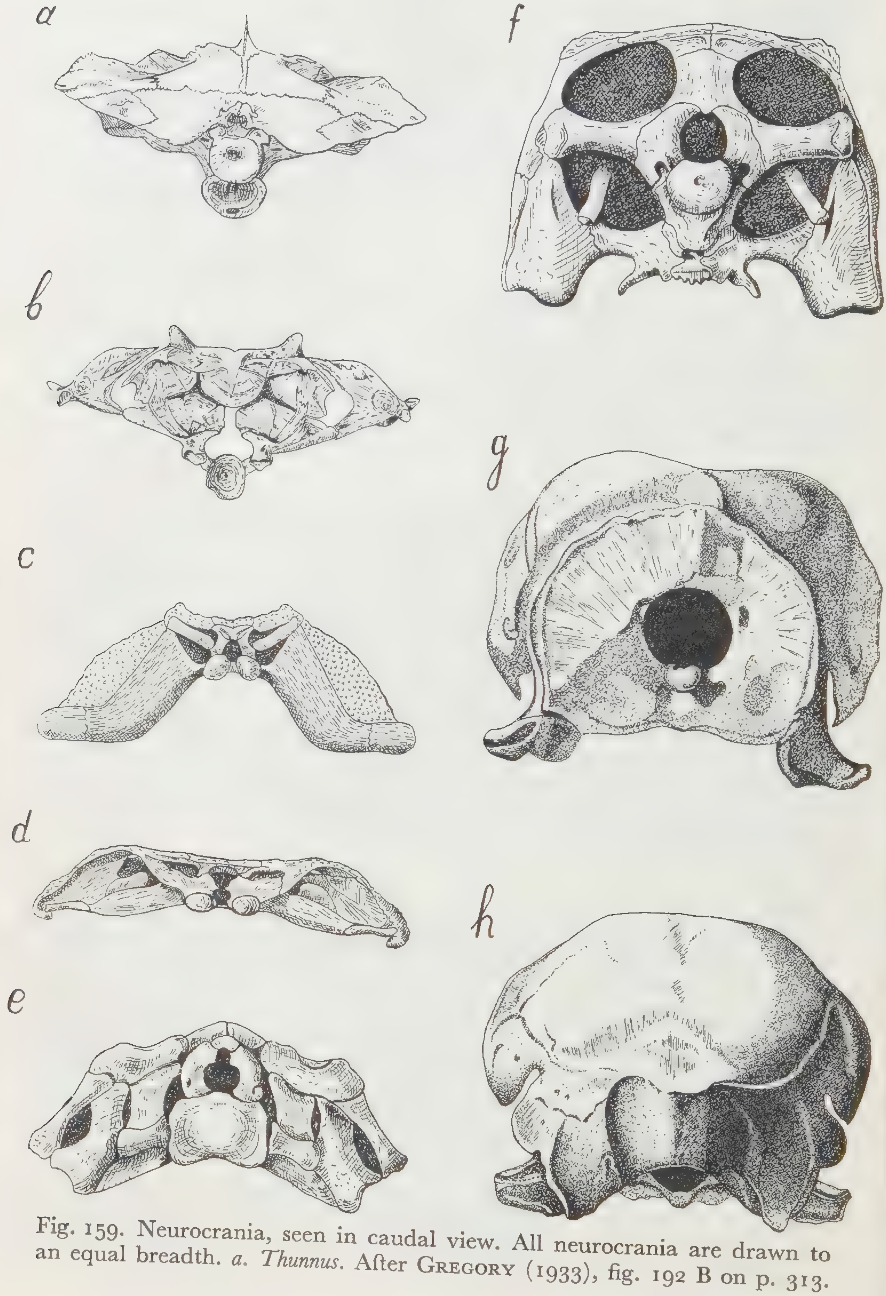
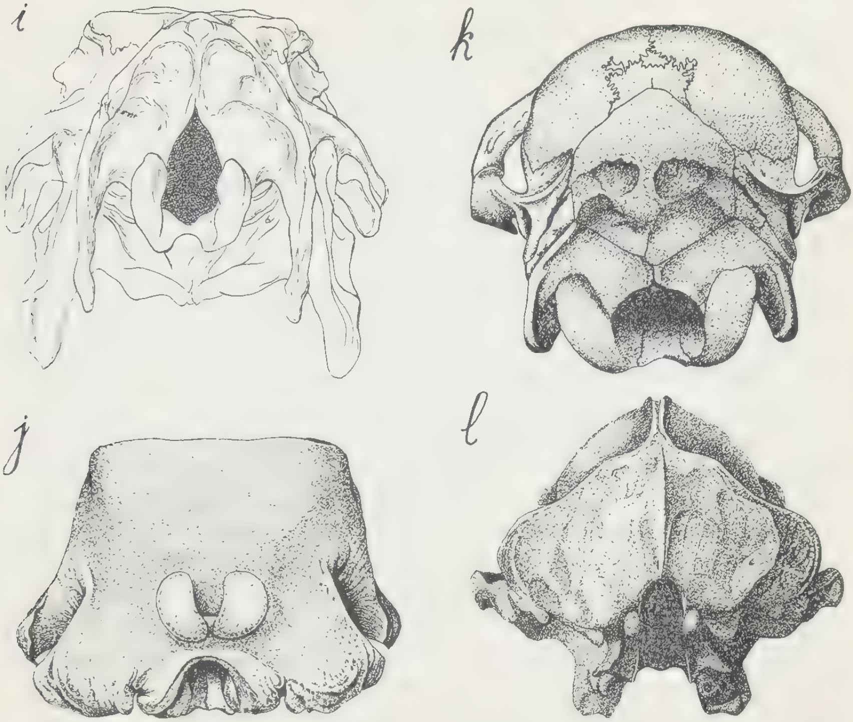


Fig. 159. Neurocrania, seen in caudal view. All neurocrania are drawn to an equal breadth. *a. Thunnus.* After GREGORY (1933), fig. 192 B on p. 313.



b. Hemitripterus. After Gregory (1933), fig. 299 B on p. 436. *c. Eryops megacephalus* Cope. 0.12×. After Abel (1919), fig. 205 on p. 277. *d. Cyclotosaurus posthumus* E. Fraas. 0.25×. After Abel (1919), fig. 189 on p. 242. *e. Stenopterygius acutirostris* (Owen). After Abel (1919), fig. 355 on p. 456. *f. Triassochelys dux* Jaekel. 0.5×. After Abel (1919), fig. 301 on p. 387. *g. Crax.* After Portmann (1950), fig. 74 A on p. 101. *h. Aquila,* After Portmann (1950), fig. 74 B on p. 101. *i. Hydrochoerus hydrochaeris* (L.). After Giebel in Bronn (1874–1900), Table XXIV, fig. 1 b. *j. Physeter.* After an original drawing by M. A. Koekkoek in the coll. of R.M.N.H. Leiden. *k. Equus caballus* L. New born. After Sisson & Grossman (1947), fig. 30 on p. 52. *l. Pongo pygmaeus* (Hopp.). After Giebel in Bronn (1874–1900), Table II, fig. 9.

than in the larger species; a relatively larger cross section at this transition will probably be accompanied by a relatively larger foramen occipitale.

b. The position

In stages of development

The position of the foramen occipitale may change in the course of ontogeny. In most of the Primates *e.g.*, but also in many other Mammalia, a postembryonal shifting of the foramen occipitale occurs (STADTMÜLLER, 1936, p. 991).

In adult animals

In Pisces (see my figs 17, 18, 19, 73, 159 *a*, *b*), Amphibia (see my figs 20, 97 *b*, 159 *c*, *d*) and Reptilia (see my figs 9, 10, 11, 12, 159 *e*, *f*) the foramen occipitale is situated in the caudal wall of the cerebral skull. This wall is at right angles to the axes of the brain and the medulla spinalis, which axes are each others prolongation.

Among the Reptilia † *Pterosaurus* is an exception to the rule that in the lower Vertebrata the foramen occipitale is directed caudally and not ventrally (KINGSLEY, 1925, p. 135).

In Aves with the skull type with a straight longitudinal axis, the planum occipitale and the foramen occipitale are directed caudally, but in Aves with a skull type with a curved or cracked longitudinal axis, the foramen occipitale is situated in the base of the skull and the planum occipitale is directed ventrally (MARINELLI, 1936, pp. 811, 820, 821/822, 834) (see my figs 13, 14, 15, 159 *g*, *h*, 171). In the Picidae the foramen occipitale has shifted to the ventral side, due to the fact that the cervical part of the vertebral column, like the handle of a hammer, is at right angles to the base of the skull (BÖKER, 1937, p. 30).

According to STRESEMANN (1927, p. 48) there is a connection between the size of the orbitae and a more or less uplifted or erect position of the axis of the brain, which by its direction influences the position of the foramen occipitale. In the large-eyed Striges the position of the foramen occipitale is ventral, whereas a caudal direction of the foramen occipitale occurs in groups with small eyes, such as Anseres, Galli and Psittaci.

In Mammalia a relation may be observed between the position of the foramen occipitale and the development of the brain and also with a burrowing way of living (see my figs 1, 2, 3, 4, 5, 16, 70 *b*, 107 *c*, 110 *b*, 147, 152, 153, 159 *i*, *j*, *k*, *l*, 161).

In Mammalia the great development of the brain has caused the caudal wall of the cerebral skull to rotate backwards and ventralwards, so that it slopes more or less backward and lies in *Homo* even horizontally (STADTMÜLLER, 1936, pp. 856, 865, 911, 957) (see my figs 5, 156 *c*, 161 *d*). Consequently the foramen occipitale is directed obliquely downward or even ventralward instead of caudally. In *Daubentonia* the foramen occipitale is directed downward and backward and is at an angle of 125° with the basioccipitale (OWEN, 1866 II, p. 526). In the higher species of apes several differences and transitions occur in the slope of the plane of the foramen occipitale (OWEN, 1866 II, p. 552). In *Homo* and in many Platyrrhina the foramen occipitale is directed downward (STADTMÜLLER, 1936, pp. 911, 952, 988) (see my figs 5, 156 *c*, 159 *l*, 161 *d*). According to STADTMÜLLER (1936, p. 952) the ventral position of the foramen occipitale in *Homo* is due to a downward deflection of the base of the skull in the region of the fossa hypophyseos as well as to the influence of the erect position of the axis of the body. In *Tarsius* the forward shifting of the foramen occipitale, according to STADTMÜLLER (1936, p. 990), must be due to the high degree of development of the brain and to the vertical position of the axis of the body. But the situation of the foramen occipitale does not depend on the direction of the vertebral column alone, other factors play a part, without an apparent causal connection with the bipedal locomotion, but rather with the development of the facial skull evolved under the cerebral skull (STADTMÜLLER, 1936, pp. 953, 991). As the degree of development of the brain influences the inclination of the plane of the foramen occipitale, as well as the slope of the lamina cribrosa, WEBER (1927 I, p. 217) could point out that with progressive development of the brain, the angle between basis cranii and the plane of the condyli occipitales becomes more obtuse to approximately the same degree as the angle between basis cranii and lamina cribrosa.

In burrowing Mammalia, as *Talpa*, *Condylura*, *Chrysochloris*, *Notoryctes*, *Geomys etc.*, the skull and the cervical vertebral column are at an angle of about 60°–70° with each other, which fact is connected with the use of the head as a hammer (BÖKER, 1935, pp. 174/175). Doubtless this has an influence upon the slope of the plane of the foramen occipitale.

c. Homology and non-homology

These differences in size and position of the foramen occipitale are apparently practically independent of the fact that the caudal limit of the skull and consequently also the foramen occipitale in several large groups of Vertebrata is not homologous in the strict sense of the word.

54. CONDYLI OCCIPITALES

a. The size

The condyli occipitales may be called absolutely and relatively small and consequently they have little influence upon the architecture of the skull.

Yet the fact whether condyli are present or lacking is very important for the general architecture of the skull. When they are present, as in Tetrapoda, the head is very mobile, which is connected with certain ways of seizing the food, defence *etc.* with all their consequences for the architecture of the skull. When condyli occipitales are wanting, as in most Pisces, this is accompanied by torpedo-type and streamlined surface of the body and of the dermatocranium, with the absence of an externally visible neck, with the head functioning as a bow *etc.* and this means various influences upon the architecture of the skull.

As already mentioned, condyli occipitales are wanting in most Pisces, except in a number of species living on the bottom (MARINELLI, 1936, p. 220) (see my figs 73, 159*a*, *b*). The condyli occipitales, occurring in Batoidei, *Chimaera* and *Squatina*, have forerunners in protuberances on either side of the chorda in a few Squaliformes (MARINELLI, 1936, p. 220; HOLMGREN & STENSIÖ, 1936, p. 316; STADTMÜLLER, 1936, p. 501). Moreover GREGORY (1933, pp. 178, 435) also mentions the tripartite occipital condyle and the three occipital condyles in the typical percomorphs resp. in the typical acanthopts. He refers in this case to the picture of one of the Scorpaenoidei, which according to certain authors are allied with the percomorphs (p. 436, see also p. 321; fig. 299). Entirely different is the pseudo-occipital condylus in *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*), which is a portion of a vertebral centrum (p. 178). This is accompanied by a comparatively small and weak articulation between the skull and the vertebral column in *Gonorhynchus gonorhynchus* (L.) (p. 178). In most Teleostei the junction of the occipital region of the skull with the vertebral column is firm, a.o. by coalescence of vertebrae (GREGORY, 1933, p. 442).

The absolute size

The absolute size of the condyli occipitales may always be called small, though they are absolutely larger in large animals than in small ones and the reverse.

The relative size

The relative size of the condylus occipitalis varies.

We mention in this connection the single condylus in Sauropsida (see my figs 9, 10, 45, 159 *e*, *f*, *g*, *h*) and a few primitive † Stegocephala, the condylus tripartitus in † Anomodontia and in *Chelonia* and the paired condyli of most † Stegocephala (see my figs 38, 159 *c*, *d*), of the Amphibia (see my figs 20, 97 *b*), † Theromorpha and Mammalia (see my figs 58, 70, 107, 110, 147, 150, 152, 153, 156 *c*, 159 *i*, *j*, *k*, *l*, 161, 168, 169, 170).

In Aves the size of the condylus occipitalis depends on the size, the weight and the carriage of the head (MARINELLI, 1936, pp. 813/814). In the avian type of skull with a straight longitudinal axis the condylus is large and distinctly stalked. In the other type with a curved or cracked longitudinal axis the condylus is small and sessile (MARINELLI, 1936, p. 814) (see my figs 13, 14, 159 *g*, *h*, 171).

b. The position

The position of the condyli occipitales varies [1]. We mention the position of the single condylus occipitalis medially upon the basioccipitale, from which it may transgress upon both exoccipitalia and on the lateral position of the paired condyli occipitales on the exoccipitalia, which may be the starting point of a transition to a more medial position in which the condyli transgress upon the basioccipitale, *etc.*

In the typical acanthopts the articular surfaces of the three occipital condyles are inclined toward each other; in the side view the half downwardly-facing exoccipital condyles and the half upwardly-facing basioccipital condyle are inclined toward each other at an angle of about ninety degrees; this prevents dislocation of the neck and consequent strangulation of the spinal cord (GREGORY, 1933, p. 436).

c. Homology and non-homology

When comparing the size and position of the condyli occipitales we must bear in mind that there are different opinions concerning the homology of the several types of condyli, a.o.

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[1] On the place of the condyli occipitales, see: A. H. SCHULTZ (1942). Conditions for balancing the head in primates. Amer. J. phys. Anthrop., **29**, pp. 483—497. (Postwar addition in the manuscript)

in connection with differences in the position of the caudal limit of the skull (Stadtmüller, 1936, pp. 842/843, 847).

55. AUDITORY OSSICLES

a. The size

Absolutely as well as relatively, the size of the auditory ossicles is always very small and accordingly their importance for the architecture of the skull is slight. But the fact of their presence respectively absence is connected with many and important architectonic differences in the skull, because it is connected with terrestrial life, or at least with descent from terrestrial ancestors.

The absolute size of the auditory ossicles in Tetrapoda is always very small.

The relative size of the auditory ossicles is also small, at least in adult skulls. In young ontogenetic stages they can be relatively much larger (Van der Klaauw, 1924).

b. The position

The proximal end of the auditory ossicles is always situated against the otic region of the cerebral skull, the distal end lies in the tympanic membrane. For the rest there are several rather important differences in the position.

The operculum in Amphibia (see my fig. 145) can be situated more or less in the same place as the basal plate of the stapes. The position of the extracolumella of the Sauropsida is in several respects different from that of incus and malleus, though both are situated between the distal end of the stapes and the membrana tympani. The ossicles of Paauw and Spence in Mammalia are situated in places, where remnants of the extracolumella might be expected (Van der Klaauw, 1923, 1924).

In some cases stapes and quadratum are in contact, *viz.* in aquatic Reptilia and in Cetacea, which fact is connected with the conduction of sound waves by bone in these aquatic animals.

c. Homology and non-homology

The differences in size between ontogenetic and adult stages are comprehensible in the light of the theory of Reichert, which derives malleus and incus respectively from the articulare and the quadratum, which are both large skeletal elements.

The differences in position between extracolumella on one side and incus and malleus on the other, are also explained by Reichert's theory, because according to this theory they are different skeletal elements. The resemblance in position between the extracolumella and the ossicles of Paauw and Spence results from their homology (Van der Klaauw, 1923, 1924). The difference in position between the basal plate of the stapes and the operculum is a consequence of the fact that they are not homologous.

56. SKELETAL FRAME OF THE MEMBRANA TYMPANI

a. The size

Exact data concerning the size of the skeletal frame of the membrana tympani are lacking in the literature consulted. The influence on the architecture of the skull of this frame, which is absolutely as well as relatively small, is unimportant.

The absolute size is small, though here again there are differences and extremes. In general the size will run more or less parallel with the size of the animal.

The relative size of this frame is also small. It seems, however, that in *Rana* the size is relatively rather large.

b. The position

In stages of development

The anulus tympanicus in Salientia arises under the eye, but as a consequence of the displacement of the palatoquadratum, to which it belongs genetically, it is shifted into the otic region (Stadtmüller, 1936, p. 591).

In adult animals

In † Stegocephala and also in † Cotylosauria the incisura oticalis in the caudal border of the secundary roof of the skull can be situated far dorsalward; in this incisura oticalis the membrana tympani is extended and it can become a complete ring, a false fenestra temporalis (Stadtmüller, 1936, pp. 512, 597; Versluys, 1936, pp. 699, 707, 708, 774).

In *Rana* the anulus tympanicus is situated laterally in the regio otica. In a few genera of Salientia, as in *Hemiphractus*, *Ceratohyla* and probably also in Amphignathodontidae, the membrana tympani is situated caudally in an incisura of the temporal region of the secundary roof of the skull (STADTMÜLLER, 1936, pp. 607/608).

In Testudinides and Loricata the rim of the U- or horseshoe- or basin- or funnel-shaped quadratum to which the membrana tympani is attached, is situated laterally (VERSLUYS, 1936, p. 800) (see my fig. 160).

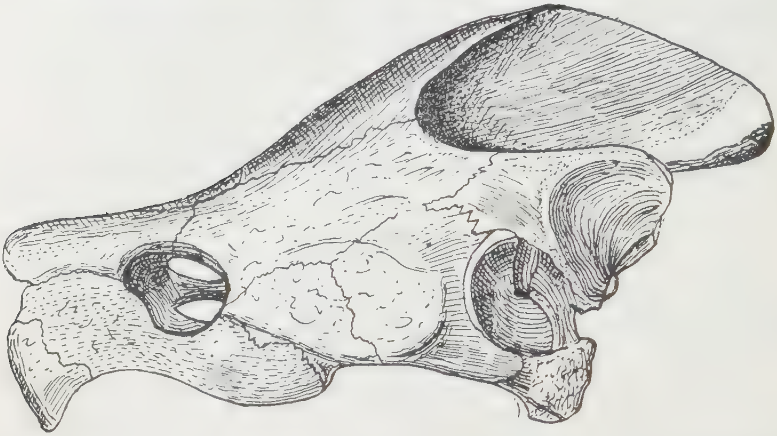

Fig. 160. *Macrochelys*. Skull seen from the left side. 0.5×. After WILLISTON (1925), fig. 30 on p. 42.

In Sauropsida the membrana tympani and consequently its frame is, according to STADTMÜLLER (1936, p. 915), situated above the joint of the jaw, whereas in Mammalia it is situated below this joint (see my figs 7, 160).

In the lower groups among the Mammalia the anulus tympanicus may have rotated rather far downward (see my fig. 107 *c*); in the higher groups it is directed more vertically again (see my fig. 113 *a*), resembling the condition in Non-Mammalia.

c. Homology and non-homology

The several skeletal frames of the membrana tympani mentioned above are not homologous in the different major groups of Tetrapoda. The cartilaginous anulus tympanicus of Salientia is not homologous with the bony anulus, which bears the same name in Mammalia, which is derived from the angulare of the

Non-Mammalia. The incisura oticalis of the † Stegocephala and † Cotylosauria is situated in the secundary roof of the skull. The frame of the membrana tympani in Testudinides and Loricata is formed by the quadratum. So it stands to reason that the position varies.

57. SKELETAL COVERING OF THE MIDDLE EAR

a. The size

The influence of the skeletal covering of the middle ear on the architecture of the skull is important, especially when it is relatively large. However, exact data on the size are not mentioned in the literature consulted.

The absolute size

The absolute size of the skeletal covering of the middle ear may be called rather large in some Reptilia, such as *Chelonia.*

Among Mammalia the bulla auditiva is very large in Cetacea and in animals living in the desert (WEBER, 1927 I, p. 75; STADTMÜLLER, 1936, p. 950). Absolutely small is the size of the bulla auditiva, not only in small Mammalia, but also in *Homo* (see my figs 156 *c*, 161 *d*).

Dealing with the size of the middle ear, we must take into account the size of its accessory cavities. The accessory cavities of the cavum tympani situated in the pneumatised adjacent elements of the skull, occur already in Loricata and in Aves (DE BURLET, 1934, pp. 1410, 1412, 1413).

In Mammalia these accessory cavities may be very large in some cases. As their size depends not only on the taxonomic group and species, but – within the species – also on age, size, race and individual characteristics of the specimen, absolute measures of the cavum tympani have little value according to DE BURLET (1934, p. 1419).

The relative size

The relative size of the bony covering of the middle ear may be called very large in some Reptilia, *e.g.* in *Chelonia* and other Testudinides (see my fig. 160).

Relatively speaking the bulla auditiva in Cetacea among Mammalia cannot be estimated large (see my fig. 161 *b*), in contrast to the bulla of several animals living in the desert. The size of the bulla is not only determined by the part the bone occupies in the covering of the soft wall of the tympanic cavity and by the degree of the inflation of the skeletal bulla, but also by the size of its dorsal edge which is situated against the base of the skull (see my figs 6, 7, 8, 35 *b*, 48 *c*, 107 *c*, 111, 147, 148, 152, 153, 154, 156 *c*, 161, 169)[1]. A relatively large bulla has its influence on the structure of the adjacent elements, as *e.g.* the processus paroccipitalis, processus posttympanicus *etc*. But, whether relatively large or small, the bulla auditiva always has a typical influence upon

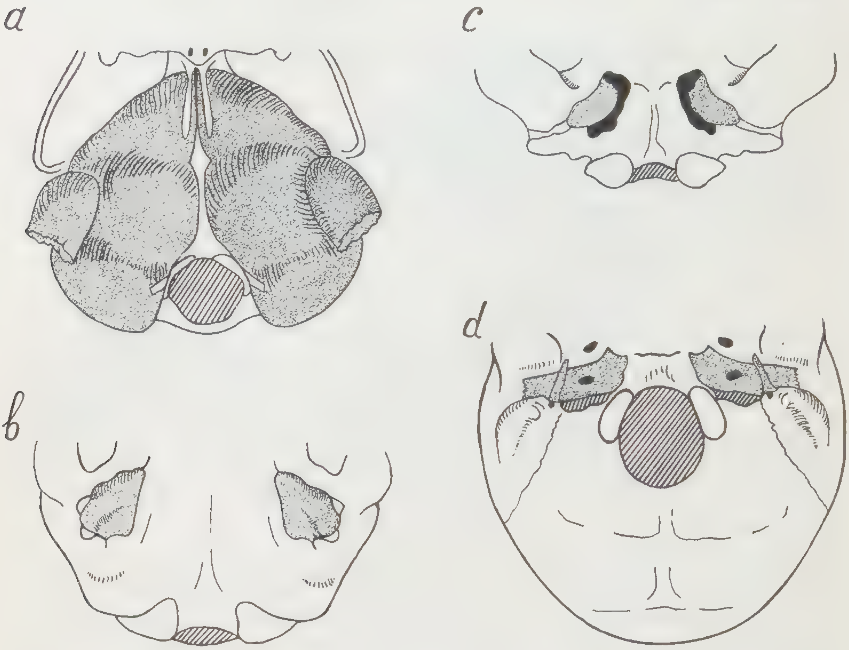

Fig. 161. Caudal parts of skulls of Mammalia, seen in ventral view. *a. Macroscelides probiscideus* (Shaw). 2.2×. After KEEN & GROBBELAAR (1941), fig. 38 on p. 318. *b. Lagenorhynchus obscurus* (Gray). 0.45×. After KEEN & GROBBELAAR (1941), fig. 42 on p. 319. *c. Hippopotamus*. 0.15×. After KEEN & GROBBELAAR (1941), fig. 9 on p. 313. *d. Homo sapiens* L. 0.35×. After KEEN & GROBBELAAR (1941), fig. 1 on p. 311.

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[1] On the size of the auditory bulla, see: J. A. KEEN & C. S. GROBBELAAR (1941). The comparative anatomy of the tympanic bulla and auditory ossicles, with a note suggesting their function. Trans. Royal Soc. South Africa, **28**, pp. 307—329. (Postwar addition in the manuscript)

the architecture of the skull, if only by the fact that it is lacking in Non-Mammalia.

Accessory cavities of the cavum tympani may be relatively large or small, but more detailed data on this matter are not given in the literature consulted.

b. The position

The position is rather divergent.

In Sauropsida in general, the quadratum which limits the cavum tympani on the rostral side, generally slants from rostroventral to caudodorsal (DE BURLET, 1934, p. 1401). In case of a very developed musculus temporalis – which is connected with the kind of food – the cavum tympani is directed obliquely from rostromedial to caudolateral (DE BURLET, 1934, p. 1402). Perhaps this is accompanied by a different direction in the adjacent elements of the skull, *i.c.* of the quadratum. The U- or horseshoe- or basin- or funnel-shaped quadratum of the Testudinides and Loricata is indeed directed lateralwards, but at the same time somewhat caudalward with its distal end (see my fig. 160).

Quite different is the position of the bulla auditiva in Mammalia, which is situated at the ventral side of the skull. This is only partly due to the fact that the membrana tympani of the Sauropsida is situated above the joint of the jaw, whereas it lies below this joint in Mammalia (STADTMÜLLER, 1936, p. 915). Within the class of the Mammalia there are rather considerable differences in the position of the bulla auditiva; it may extend more medially or more laterally, more rostrally or more caudally.

If we include in our consideration the position of the accessory cavities in Loricata, Aves and Mammalia as well, the position of the skeletal covering of the middle ear is more divergent still.

c. Homology and non-homology

The differences in size and position of the skeletal covering of the middle ear are partially due to the fact that skull elements are concerned which are not homologous. The skeletal covering of the middle ear, which is part of the quadratum, as in certain Sauropsida, is not homologous with the bulla auditiva of the Mammalia. For the occurrence of this bulla depends on the presence of a new wall, *viz.* the ventral wall of the cavum tympani of the Mammalia and so it cannot occur in Non-Mammalia (Van Kampen, 1904, 1905). But also within the class of the Mammalia there is condiserable divergence in the component skeletal elements (Van der Klaauw, 1931).

58. SKELETAL COVERING OF THE MEATUS AUDITORIUS EXTERNUS

a. Introduction

In the skeletal covering of the meatus auditorius externus we will include the osseous as well as the cartilaginous covering. The cartilaginous covering is sometimes, but not always, partly ossified.

b. The size

The absolute size

The absolute size is always small, even in large Mammalia. Generally speaking the size will be small in small Mammalia and large in large Mammalia. Yet this does not always hold true, for in case of reduction of the cartilage of the external ear, the cartilage of the meatus auditorius externus has also been reduced; this is a.o. the case in (especially large!) Cetacea (Boas, 1934, p. 1439). This is most striking in *Balaenoptera acuto-rostrata* Lacépède (*Balaenoptera rostrata*), where the cartilage of the meatus auditorius externus is only 3–4 cm long whereas the meatus itself measures 22 cm (Boas, 1934, p. 1439). In Sirenia, at least in newborn ones, the cartilage in the meatus auditorius externus is altogether lacking (Boas, 1934, pp. 1439/1440).

The relative size

As to the relative size there are considerable differences among Mammalia (see my figs 7, 26 *b*, 35 *b*, 37 *b*, 48 *c*, 99 *a*, 107 *c*, 111, 113, 147, 148, 150, 152, 153, 154, 156 *a*, *c*, 161, 169). The length of the meatus auditorius externus is connected with the breadth of the brain and the skull (Stadtmüller, 1936, p. 954). This relation is influenced by other factors. For instance this skeletal covering is relatively short in Cetacea *etc.*, where the cartilage of the meatus auditorius externus is reduced in connection with the reduction of the skeleton of the external ear.

c. The position

The skeletal covering of the meatus auditorius externus projects from the skeletal frame of the membrana tympani, against which its proximal end is situated. Concerning the exact direction in which it projects laterally, the consulted literature does not mention any data.

d. Homology and non-homology

These skeletal coverings are homologous structures in all Mammalia and consequently differences in size and position must be explained on other grounds.

59. SKELETON OF THE EXTERNAL EAR

a. Introduction

The skeleton of the external ear (see my fig. 162) is very seldom ossified (Boas, 1934, p. 1441). So we are allowed to speak of the cartilage of the external ear.

b. The size

The absolute size may be very different. We mention only the cartilage of the external ear in *Elephas* and *Equus* as opposed to that of very small Mammalia and *Homo*. The skeleton of the external ear is entirely lacking in Cetacea and Sirenia (Boas, 1934, pp. 1439/1440).

The relative size also varies very much. Relatively large is the cartilage of the external ear in *Oryctolagus* and in a number of small Rodentia with large ears. Also in *Elephas* it is relatively large.

c. The position

The skeleton of the external ear is situated on either side against the skull. The cartilage of the external ear is continuous with the cartilage of the meatus auditorius externus.

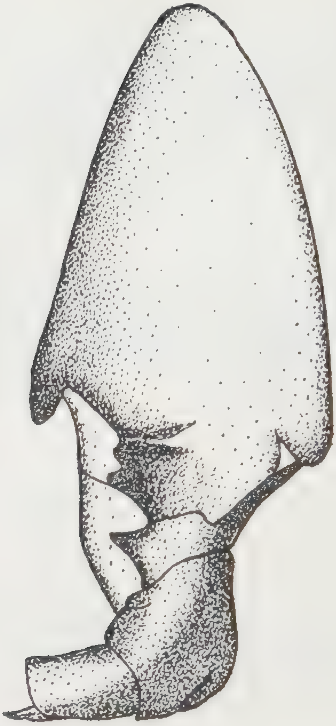

Fig. 162. Diagram of the skeleton of the external ear of a viviparous mammal. After Boas (1934), fig. 1274 on p. 1440.

d. Homology and non-homology

Differences in size and position of the skeleton of the external ear cannot be explained by a possible non-homology, for the skeleton of the external ear is homologous in all Mammalia.

60. FOSSA FOR THE DIVERTICULUM OF THE SWIM-BLADDER

a. The size

In *Tarpon atlanticus* (C. & V.) and other Isospondyli the fossa which lodged a diverticulum of the swim-bladder, is said to be deep (Gregory, 1933, p. 245).

In *Gymnarchus niloticus* Cuv. the "temporal vacuity" on the lateral wall of the cranium in the midst of the semicircular canals, which receives the "anterior bulb" of the air-bladder, much as in *Notopterus*, is said to be large (Gregory, 1933, p. 173).

b. The position

In Clupeoidea the squamosum and prooticum contain the caecal diverticula of the swim-bladder or they extend forward into the pteroticum and prooticum (Gregory, 1933, pp. 147–149, 155). Concerning *Tarpon atlanticus* (C. & V.) only Gregory (1933, p. 245) mentions the fact that the diverticulum of the swim-bladder is situated on the lateral surface of the otic region.

In *Notopterus* among the Mormyroidea portions of an air-vesicle, which is a diverticulum of the swim-bladder, are situated in a ventro-lateral vacuity in the otic region, bounded above by the opisthoticum and prooticum and internally by the basioccipitale (Gregory, 1933, pp. 169, 174). In *Gymnarchus niloticus* Cuv. the "temporal vacuity", which receives the "anterior bulb" of the air-bladder, lies in the midst of the semicircular canals on the lateral wall of the cranium (Gregory, 1933, p. 173). In *Hyodon* there are vesicles of the swim-bladder on the lateral face of the otic region of the cranium (p. 174). Concerning the Mormyridae is mentioned the extension of diverticula of the swim-bladder into the bony chamber of the inner ear, just as in Osteoglossidae and in Ostariophysi (Gregory, 1933, p. 184).

Such prolongations of the swim-bladder have thus burrowed their way into various places on the side of the cranial vault (Gregory, 1933, p. 439).

c. Homology and non-homology

The difference in size and position of the fossa for diverticula of the swim-bladder may be due to incomplete homology. Thus it is contested that the caecal diverticula of the air-bladder in the Clupeoidea are fully homologous with somewhat similar diverticula found in Ostariophysi (Gregory, 1933, p. 155). And the vesicles of the swim-bladder in *Notopterus* and *Hyodon* need not have had a common origin (Gregory, 1933, p. 174).

61. FORAMEN PINEALE S. PARIETALE

a. Introduction

In the foramen pineale are situated the pineal and parapineal organs. There are two different foramina, one in the cartilaginous primordial neurocranium and one in the dermal roof of the skull. As in the dermal roof of the skull it is generally situated between the right and left parietale, it is also called foramen parietale. It occurs in a number of Vertebrata (STADTMÜLLER, 1936, pp. 597, 598, 923).

b. The size

The absolute size is always small, whenever it occurs among Pisces (see my figs 72, 73), Amphibia (see my figs 38, 39), Reptilia and Mammalia.

The relative size is also small, though relatively speaking the foramen pineale may be comparatively well developed.

c. The position

Concerning the position with respect to a more rostral or caudal situation of this medial foramen in the cranial roof, the consulted literature mentions no exact data.

It lies in the roof of the cartilaginous primordial neurocranium in Selachii (see my figs 72, 73).

In general the foramen pineale is situated between the right and left parietalia, but sometimes it lies between the parietalia and the frontalia and sometimes between right and left frontale, whereas in a few groups a separate bone, the praeparietale, has developed in front or round about the foramen pineale (OWEN, 1866 I, p. 159; WILLISTON, 1925, pp. 11, 52; KINGSLEY, 1925, pp. 139, 193/194; NOBLE, 1931, p. 214; GREGORY, 1933, p. 107; HOLMGREN & STENSIÖ, 1936, p. 355; STADTMÜLLER, 1936, pp. 597/598, 923).

d. Homology and non-homology

The foramen pineale in the roof of the cartilaginous primordial neurocranium is homologous in all Vertebrata which show it. The same is the case with the foramen pineale in the dermal roof of the skull. Thus differences in position in both categories must be explained by other reasons than non-homology.

62. CIRCUMORBITALIA, PERIORBITALIA, CONJUNCTIVAL RING, SCLEROTICALIA, OSSIFICATIONS IN THE PALPEBRAE AND OTHER PERIORBITAL OSSEOUS RING STRUCTURES

a. Introduction

We shall treat here under one heading all the above mentioned ring-like structures round the eye composed of dermal bones. They are the circumorbitalia or periorbitalia in Pisces and † Stegocephala (see my figs 38, 39), consisting of a ring of small superficial dermal ossifications round the lateral circumference of the eye. It includes also the osseous conjunctival ring, which occurs in *Acipenser* and perhaps in some † Stegocephala. It is moreover the bony circumcorneally situated sclerotical or scleral ring of the scleroticalia, which is found in other † Stegocephala, which is typical for most of the Sauropsida (see my figs 103, 163), and whose occurrence seems already probable in Crossopterygii (FRANZ, 1934, pp. 994, 996, 1023, 1025, 1026, 1093, 1095, 1117, 1119, 1185, 1186, 1204; STADTMÜLLER, 1936, pp. 602, 627, 629/630). The remnants of the dermal orbital ring in Aves also belong here (FRANZ, 1934, pp. 1128, 1132, 1133, 1134/1135; MARINELLI, 1936, pp. 819, 837). Also the ossifications in the palpebrae, dermal plates along the upper edge of the orbita in Sauria. And finally the periorbital osseous rings, which differ from the scleroticalia in not consisting of uniform bony plates; they often occur in living and fossil Pisces and in fossil Amphibia and Reptilia (FRANZ, 1934, p. 1186).

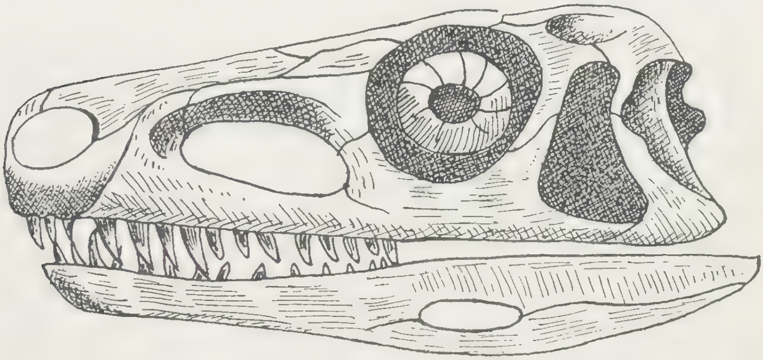

Fig. 163. *Euparkeria capensis* Broom. Skull seen from the right side inverted. After ABEL (1919), fig. 417 on p. 526.

b. The size

Exact data concerning the absolute as well as the relative size of the circumorbitalia and other rings of dermal ossifications round the eye are entirely lacking.

The absolute size

The absolute size of all the skull elements mentioned in the heading of this paragraph corresponds with the absolute size of the eye and consequently – with certain restrictions – with the absolute size of the orbita. These rings vary from small to large, which partly determines their importance for the architecture of the skull. But perhaps this significance depends still more on the fact whether or not a certain ring is present.

In the ring of circumorbitalia broadening may occur either all round the ring or locally (*e.g.* in the lacrimale), by which the absolute size may increase considerably. However we shall treat this point together with the relative size.

The relative size

As all the osseous rings mentioned in the heading of this paragraph correspond in size with the size of the eye, their relative size will also be in accordance with the relative size of the eye and consequently – with certain restrictions – with the relative size of the orbita. The space between the eye and the inner wall of the orbita is significant in this connection. Thus the considerable relative size of the eye in Aves, is said to be the cause of the nearly total disappearance of the dermal orbital ring (MARINELLI, 1936, pp. 819, 837).

Concerning the relative size of the ring of circumorbitalia in Pisces, we are very well informed thanks to the extensive study of GREGORY (1933).

In a number of cases this ring of circumorbitalia is not complete, generally the dorsal part is lacking; in other cases more elements are absent, *e.g.* also in the ventral part.

In some cases the ring of circumorbitalia is narrow along the whole of its length and even the lacrimale projects hardly or not at all beyond its circumference. This is the case in *Dorosoma erebi* (Gthr) (*Chatoessus erebi*) (fig. 39) (see my fig. 29), *Myripristis murdjan* (Forsk.) (fig. 111) and *Priacanthus* (fig. 120).

In many cases the lacrimale, being much broader, projects beyond the circumference of the narrow ring; this occurs *e.g.* in *Lates niloticus* (Gmel.) (figs 114, 298) (see my fig. 115), *Mugil cephalus* L. (fig. 138), *Osphronemus* (fig. 147), *Antigonia capros* Lowe (fig. 149 B), *Scorpis* (fig. 150), *Chaetodipterus faber* (Brouss.) (fig. 152 A), *Chaetodon ocellatus* Bl. (fig. 155), *Trachinotus falcatus* (L.)

(fig. 178), *Brama rayi* (Bl.) (fig. 182) (see my fig. 83), *Coryphaena* (fig. 183), *Rhachycentron* (fig. 186) (see my fig. 120), *Echeneis* (fig. 199), *Malacanthus* (fig. 235), *Eleginops* (fig. 238) and *Anarhichas* (fig. 255).

In some cases the circumorbital ring is relatively rather broad along the whole of its length, *e.g.* in *Polydactylus* (fig. 144), *Scomberoides tolooparah* (Rüpp.) (fig. 180) and *Coryphaenoides* (fig. 262).

A local broadening of the ring of circumorbitalia occurs in countless cases.

A broadening of the caudal and caudoventral part of the ring is brought about in two ways.

The † Semionotidae, as † *Acentrophorus*, † *Dapedius*, † *Semionotus*, † *Lepidotus etc.* show two rows of large orbital plates, called here the circumorbitalia and the postorbitalia; above the eye there are several supraorbital plates (Gregory, 1933, pp. 125, 439, figs 21 B, 22 A, B). Both rows also occur in *Lepisosteus* (fig. 24 A) (see my figs 51, 65), † *Furo* (*Eugnathus*) (fig. 27), *Amia calva* L. (fig. 28) and in the palaeoniscoid † *Perleidus* (fig. 21 A).

Another type of broadening of the caudal and caudoventral part of the ring is effected by the circumorbitalia alone; this is the case in † *Portheus molossus* Cope (fig. 36), *Chanos chanos* (Forsk.) (*Chanos salmoneus*) (fig. 44), *Heterotis niloticus* (Cuv.) (fig. 58), *Notopterus* (fig. 61), *Brycon dentex* Gthr (fig. 70), *Astroscopus* (fig. 247) (see my fig. 42) and especially in *Arapaima gigas* (Cuv.) (fig. 59), *Erythrinus unitaeniatus* Spix (fig. 67) (see my fig. 28) and *Hydrocyon lineatus* Blkr (fig. 69) (see my fig. 86).

A broadening of the caudal circumorbitalia in a caudal direction occurs in † *Palaeoniscus macropomus* Agassiz (fig. 12 B), *Scomber* (fig. 188) and especially in *Amia calva* L. (fig. 28) and in *Osteoglossum* (fig. 57) (see my fig. 116).

A considerable broadening of the ventral circumorbitalia in a caudal direction occurs in Scorpaenoidei (pp. 428, 434), as in *Scorpaena plumieri* Bl. (fig. 201), *Scorpaena scrofa* L. (figs 116, 203) (see my fig. 79), *Pterois* (fig. 205), *Pelor* (fig. 206) (see my fig. 124), *Synanceja* (fig. 207), *Hexagrammos* (fig. 209), *Ophiodon* (fig. 210), *Platycephalus* (fig. 211), *Cottus octodecimspinosus* (Mitchill) (fig. 212), *Aspicottus* (*Enophrys*) (fig. 216), *Cyclopterus* (fig. 217), *Peristedion* (fig. 220) (see my fig. 75) and *Dactylopterus* (*Cephalacanthus*) (figs 222, 223), while in *Prionotus* (fig. 218) and *Trigla* (fig. 219) moreover the ring is also very high in the same place.

A ventrally directed broadening of the ventral part of the circumorbital ring occurs in *Petrocephalus bane* (Lac.) (fig. 64) (see my fig. 88) and *Uranoscopus* (fig. 246).

A broadening of the rostral or rostroventral part of the circumorbital ring is nearly always due to a lengthening of the lacrimale. A broadening in the same place, due to another component than the lacrimale, occurs in *Teuthis virgata* (C.V.) (fig. 159).

Such a broadening due to the lacrimale is, however, extremely common among Pisces (Gregory, 1933, p. 88 counts this skull element, which can be so divergent in its relations, among the circumorbitalia). We shall not enumerate the extraordinary high number of cases, but limit ourselves to the following. It is typical that Gregory (1933, fig. 7) (see my figs 114, 143 *c*) in his composite diagram, based upon the study of skulls of about fifty species of teleosts, pictures the lacrimale as a long and rather broad element, which broadens the circumorbital ring considerably in this place. This is characteristic of the lacrimale and consequently of the circumorbital ring in its place already in the palaeoniscoid † *Platysomus parvulus* Williamson (fig. 15 B) (see my figs 90, 143 *b*) and in the amioid † *Furo* (*Eugnathus*) (fig. 27). But in countless Teleostei similar conditions occur as well. We only shall quote examples of three special conditions, *viz.* cases in which the lacrimale is long and narrow and projects relatively far rostralwards, cases in which the lacrimale extends over a very large area and finally cases in which this can even be called an extremely large surface. Long and narrow and projecting far rostralwards is the lacrimale in *Gonorhynchus gonorhynchus* (L.) (*Gonorhynchus greyi*) (fig. 66) (see my fig. 64), *Esox masquinongy* Mitchill (fig. 95 A) (see my fig. 30), *Gasterosteus spinachia* L. (fig. 103), *Sphyraena barracuda* (Walbaum) (fig. 141), *Angelichthys ciliaris* (L.) (fig. 153), *Pomacanthus arcuatus* (L.) (fig. 154), *Hepatus triostegus* (L.) (fig. 156), *Rhachycentron* (fig. 186) (see my fig. 120), *Istiophorus* (fig. 196), *Mastacembelus* (fig. 233), *Gadus* (fig. 258 A), *Lota* (fig. 258 B), *Prionotus* (fig. 218), in which the lacrimale projects rostralwards very far indeed and in *Peristedion*, in which the growth momentum of the lacrymal bones has resulted in a pair of long processes which project far in front of the nasalia (p. 343, fig. 220) (see my fig. 75). – A relatively very extensive lacrimale occurs in *Chirocentrus dorab* (Forsk.) (fig. 34), *Fundulus* (fig. 96 A), *Micropogon* (fig. 125), *Gerres lineatus* (Humboldt) (fig. 126), *Microspathodon chrysurus* (C.V.) (fig. 128), *Chaetodipterus faber*

(Brouss.) (fig. 152 A), *Pterois* (fig. 205), *Ammodytes* (fig. 234), *Pinguipes* (fig. 236 A) and *Blennius* (fig. 252). – Extremely large is the surface of the lacrimale in *Haemulon* (fig. 121) (see my fig. 127), *Lachnolaimus maximus* (Walbaum) (fig. 130) (see my fig. 129), *Cheilodactylus spectabilis* Hutton (fig. 136) and *Scomber* (fig. 188).

c. The position

In the introduction we already made some remarks upon the position of the osseous rings mentioned in the heading of this paragraph.

They are all situated round about the eye and consequently at the circumference of the orbita. Concerning the circumorbitalia of Pisces, GREGORY (1933, p. 428) points out that in ontogenetic stages the suspensorium is curved forward and this curvature is followed by the opercular series, which is probably the explanation of the "circumorbital" arrangement in the oldest † Protospondyli of the circum- and suborbitalia, so that traces of the embryonic arrangement persist in the adult stages. The circumorbitalia are superficial dermal ossifications, situated round the circumference of the lateral part of the eye. The conjunctival ring is also situated round about the eye, but in the conjunctiva. The osseous sclerotical or scleral ring of scleroticalia lies circumcorneally. The ossicles in the palpebrae of the Sauria are situated along the dorsal border of the orbita.

Along their periphery the bony elements treated in this paragraph border on the skull elements situated round the orbita. So we may refer to the discussion of the position of the orbita. Two points, however, must be specially mentioned here, *viz.* the position of the lacrimale, extending far into the snout and secondly the position of the circumorbitalia in relation to the operculum in Pisces.

As to the position of the circumorbitalia in relation to the praeoperculum, GREGORY (1933, pp. 428, 434) points out that in ontogenetic stages the suspensorium is curved forward, which brings the entire opercular fold into close proximity with the eye and with the circumorbital bones. This suggests how readily one of the circumorbital bones could form an adhesion of its posterior border to the rim of the praeoperculum, such as we find in the Scorpaenoidei. Another way of filling the space between the eye and the rim of the praeoperculum is found in *Arapaima e.g.*, where several of the circumorbital bones behind the eye share the increased length between the eye and the praeoperculum. The space between the opercular flap and the orbita increases in many groups as the individual fish becomes older. Then in a number of cases the contact between the nearest circumorbital bone and the praeoperculum is retained, as in *Arapaima* and the Scorpaenoidei, in other groups this contact is not retained.

d. Homology and non-homology

In a number of lower Pisces we have come to know besides the circumorbitalia a series of postorbitalia, which, however, according to Gregory (1933, p. 89) are not equivalent to the true postorbitale of the Tetrapoda, which is derived from the inner or circumorbital row.

The osseous conjunctival ring may perhaps be derived from the circumorbitalia by assuming a displacement and the same applies to the osseous sclerotical or scleral ring of scleroticalia. Also the dermal orbital ring in the Aves may be derived from the periorbital ring of circumorbitalia.

Probably the palpebral ossicles along the dorsal border of the orbita in Sauria have a different origin, they are a later formation of the rim. Perhaps this is comparable with the periorbital osseous rings, which do not consist of uniform osseous platelets and are therefore different from the scleroticalia (Franz, 1934, p. 1186).

63. CARTILAGE IN THE SCLERA

a. Introduction

In this paragraph on the cartilage in the sclera, we shall include three types of cartilaginous formations in the sclera, *viz.* the proper sclera cartilage; the "ossicle of the nervus opticus" ("Sehnervknochen") or hinder deeper sclerotical ring and the cartilage in the external layer of the bulbus oculi in *Notoryctes.*

The proper sclera cartilage (Marinelli, 1936, p. 218) is not yet developed in Marsipobranchii (Franz, 1934, pp. 998, 1002, 1022), but it is present in Selachii and countless higher Pisces (Franz, 1934, pp. 1009, 1022, 1023, 1025, 1026, 1027, 1029, 1051, 1054, 1055, 1058, 1059, 1060, 1064; Holmgren & Stensiö, 1936, pp. 237, 328, 349), in many Amphibia (Franz, 1934, pp.

1065, 1079, 1083, 1084, 1086, 1089; STADTMÜLLER, 1936, pp. 544, 545) and in most of the Sauropsida (FRANZ, 1934, pp. 1093, 1095, 1106, 1107, 1109, 1116/1117; MARINELLI, 1936, p. 820). Among the Mammalia it occurs only in the Monotremata (FRANZ, 1934, pp. 1209, 1257; STADTMÜLLER, 1936, pp. 544/545, 891). Now and again ossification of this scleral cartilage occurs. This occurs already in Pisces (FRANZ, 1934, p. 1029; STADTMÜLLER, 1936, p. 630). In the passages where FRANZ (1934, pp. 1027, 1048, 1049, 1051, 1053, 1056, 1057, 1060) mentions bone in the sclera in a number of Teleostei, it is not quite clear, whether ossification of the scleral cartilage is meant. But concerning *Scomber scombrus* L. FRANZ (1934, pp. 1057/1058) indeed remarks that the scleral ossification ("Skleraknochen") of this species resembles the sclera cartilage ("Skleraknorpel") of the Selachii. Among the Amphibia ossification of the sclera cartilage is known for the adult *Triturus pyrrhogaster* (Boie) (*Diemictylus*); it also occurred in † *Branchiosaurus* (*Protriton*), in which the ossification resembled a sclerotical ring (FRANZ, 1934, p. 1079; STADTMÜLLER, 1936, p. 545).

By the ossicle of the nervus opticus ("Sehnervknochen") or hinder (deeper) sclerotical ring is understood an ossification in the sclera cartilage, which occurs in some Aves (FRANZ, 1934, pp. 1133/1134; BÖKER, 1937, p. 30). Comparable with this ossicle are a few small bones in the hind segment of the eye in † *Branchiosaurus* (*Protriton*), which probably are also ossifications of cartilage (FRANZ, 1934, pp. 1185/1186).

The third type of cartilaginous formations to be treated in this paragraph are small pieces of cartilage in the external layer of the bulbus oculi in *Notoryctes typhlops* Stirling; they often occur at the distal side of the eye as well (FRANZ, 1934, pp. 1209, 1257, 1264; STADTMÜLLER, 1936, p. 891).

All the formations of cartilage in the sclera have very little importance in relation to the architecture of the skull, if only by their very small size. If they have any significance it is by their presence or absence in general.

b. The size

Exact data concerning the size of the cartilage in the sclera are lacking.

The absolute size

The absolute size is determined by the absolute size of the sclera of the eye and consequently also by that of the eye itself. More details can be inferred from the data given below in the discussion of the relative size.

The relative size

The relative size of the proper sclera cartilage corresponds in general with the relative size of the sclera and consequently with that of the eye. This applies especially to the length and breadth or – better perhaps – to the diameter; as to the thickness of the sclera cartilage, it is a somewhat different case, as we shall see below.

As to the diameter of the proper sclera cartilage we observe that it may be cup-, basin-, plate- or ring-shaped, but it may also consist of separate pieces of cartilage. The form usually depends on the taxonomic group, even on the species; sometimes again it is related to the ontogenetic stage (FRANZ, 1934, pp. 1009, 1056, 1059, 1064, 1065, 1079/1080, 1084, 1085, 1089, 1095, 1097, 1106, 1108, 1120, 1133; HOLMGREN & STENSIÖ, 1936, p. 328; STADTMÜLLER, 1936, p. 545).

As to the thickness of the proper sclera cartilage, usually this cup, basin, plate or ring is very thin. But among the Plagiostomata with a very spacious (and especially deep) orbita, the sclera cartilage is thick, as in Batoidei, in which the eye ball lies at some distance from the skull, while – the other way round – when the orbita is narrow the sclera cartilage is thinner (FRANZ, 1934, p. 1019). The same principle is demonstrated in the small eyed *Acipenser sturio* L. (FRANZ, 1934, p. 1023). Also in certain Amblyopsidae relatively enormous, irregular formations of cartilage occur in the sclera (FRANZ, 1934, p. 1053). *Megalobatrachus japonicus* (Temm.) (*Cryptobranchus japonicus*) has, according to FRANZ (1934, p. 1083), a strikingly colossal sclera cartilage cup, which dwarfs every other scleral thickening accompanying small eyes. Also in *Cryptobranchus alleganiensis* (Daud.) (*Menopoma*) the sclera cartilage is very thick (FRANZ, 1934, p. 1084). Probably BÖKER's observation (1937, p. 21) that in Aves the cartilaginous-osseous frame ("Gerüst") of the scleral ring is the stronger, as the bulbus oculi is longer, refers to this skeletal formation in the sclera.

The ossicle of the nervus opticus ("Sehnervknochen") or hinder (deeper) sclerotical ring in some Aves is also relatively very small. And so are the pieces of cartilage in the external layer of the bulbus oculi in *Notoryctes typhlops* Stirling.

c. The position

The proper sclera cartilage lies in the sclera. In all groups it is detached, except in Selachii, in which it is attached to the eye stalk (Holmgren & Stensiö, 1936, p. 237).

The ossicle of the nervus opticus ("Sehnervknochen") or hinder (deeper) sclerotical ring is situated round the nervus opticus; so it lies in the back part of the eye.

The pieces of cartilage in *Notoryctes* lie in the external layer of the bulbus oculi and they often occur at the distal side of the eye.

d. Homology and non-homology

The sclera cartilage is not homologous with the osseous ring of the scleroticalia, treated in the preceding paragraph. The ossicle of the nervus opticus ("Sehnervknochen") or hinder (deeper) sclerotical ring is derived from the sclera cartilage.

The cartilage in *Notoryctes* is something quite different, as results from its position in general and also from the fact that it may occur at the distal side of the eye.

64. FORAMEN ANTORBITALE OR FENESTRA ANTORBITALIS

a. Introduction

The foramen antorbitale or fenestra antorbitalis or preorbital fenestra occurs in Aves and in some Archosauria. Its function is not known; perhaps it serves the passage of a jaw muscle or the purpose may be to keep down the weight or again it may simply mean a place which is not subject to pressure and tension (Versluys, 1936, pp. 722/723, 788, 789, 792, 793; Marinelli, 1936, p. 826). Though the function is not known, we shall all the same dedicate a short paragraph to this foramen, although this paper deals with the skull from the functional aspects of its components.

b. The size

Exact data concerning the size of this foramen were not met with in the literature consulted.

The size may be, absolutely as well as relatively, very small, but also very large.

c. The position

The foramen antorbitale or fenestra antorbitalis is situated rostrally from the orbita. Further details concerning the position are not mentioned in the literature consulted.

d. Homology and non-homology

I have not come across opinions, according to which this foramen would not be homologous in all groups in which it occurs.

65. SKELETAL LID OF THE EXTERNAL NOSTRIL

a. Introduction

As a skeletal lid on the external nostril may serve the os nariale *s.* septomaxillare, *viz.* when this element of the skull is situated at the surface and against one of the borders of the skeletal external nostril, which consequently is partially closed by it. However, the os nariale *s.* septomaxillare probably has in the first place the function of the attachment of the musculus dilatator naris accessorius and has, besides this, a supporting function (plica obliqua) (STADTMÜLLER, 1936, pp. 623, 624). But we shall not treat those cases in which the os nariale only serves as the skeletal lid of the external nostril separately.

The os nariale *s.* septomaxillare occurs in Teleostei, Amphibia, Reptilia and lower Mammalia (VERSLUYS, 1936, pp. 709, 774; STADTMÜLLER, 1936, p. 928).

The influence of the os nariale or septomaxillare on the architecture of the skull is slight.

b. The size

The os nariale *s.* septomaxillare sometimes has a rather considerable size, absolutely as well as relatively. Exact data, however, are lacking in the literature consulted.

c. The position

The os nariale *s.* septomaxillare is situated in the external nostril, sometimes superficially, sometimes deeper, sometimes at one border, sometimes at the other border of the nostril.

d. Homology and non-homology

Whether the differences in position may be due to non-homology is unknown to me.

66. WEAPONS ON THE HEAD

a. Introduction

In this paragraph we shall discuss several weapons on the head, by which are meant appendages and protuberances of and on the skull, which are used as weapons and also the places of attachment and support for such weapons on the skull. It stands to reason that these appendages may have other functions as well, *e.g.* in connection with sexual display.

In this paragraph we shall treat the spikes, spines and thorns which adorn the skulls of several groups of Teleostei, such as the Scorpaenoidei, Trachinoidei and Batrochoidiformes (Haplodoci) *etc.* (see my figs 75, 79, 115, 117, 118, 124, 146). GREGORY (1933, p. 427) observes that such spikes have the appearance of being useful either as defensive weapons (when moved by the wriggling of the body) or as "skids" upon which the body rests, as in *Dactylopterus* (fig. 223), or as accessory braces for a pelvic adhesive organ, as in *Gobiesox* (figs 249, 250) and in *Callionymus* (fig. 242).

Among Reptilia we mention the horns in a number of † Ceratopsia, *etc.* (WILLISTON, 1925, pp. 9/10) (see my figs 164, 165).

Among the Aves occur protuberances on the upper bill, to which may correspond an osseous protuberance and also bony knobs and protuberances at other places of the skull (see my fig. 15).

In Mammalia the following formations belong here: the horncores in Cavicornia; the antlers with the bony pedicle in Cervidae; the bony protuberances in Giraffidae; the bony knob under the horn of Rhinocerotidae a.s.o. (STADTMÜLLER, 1936, pp. 924 ff., 947 ff., 951, 952, 955) (see my figs 58, 99, 112, 150).

b. The size

Exact data on the size of the weapons on the head have not been found by me in the literature consulted.

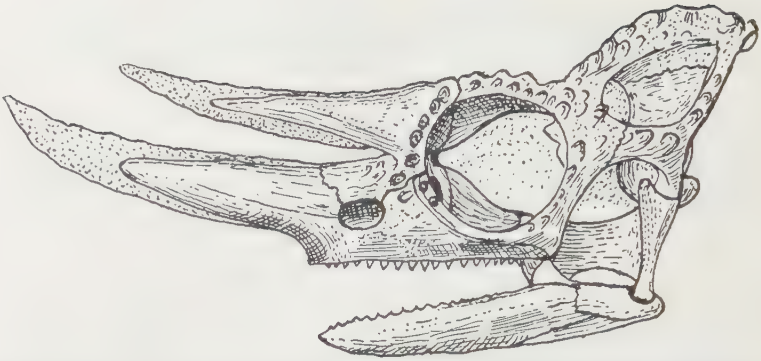

Fig. 164. *Chamaeleo.* Skull seen from the left side. Nat. size. After WILLISTON (1925), fig. 55 D on p. 68.

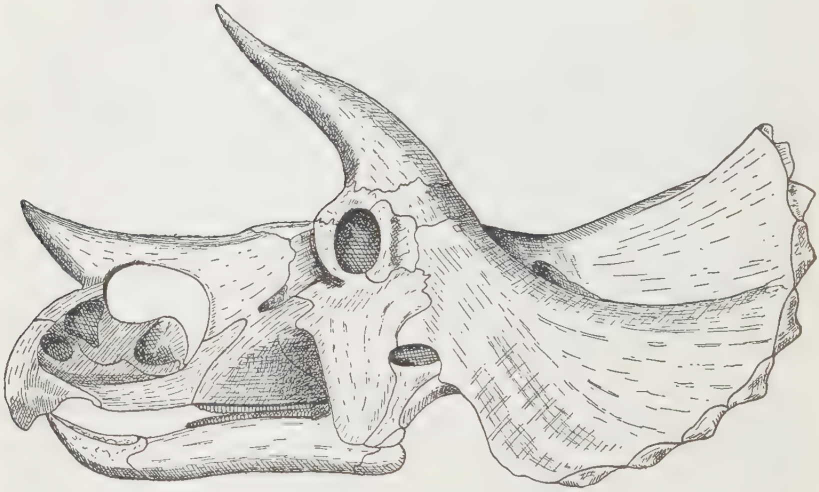

Fig. 165. *Triceratops.* Skull seen from the left side. After ABEL (1919), fig. 516 on p. 652.

The absolute size

In Pisces even the relatively largest spikes can still be called small in the absolute sense.

Absolutely large are the horns of a number of † Ceratopsia. So are the antlers with their bony pedicles in Cervidae. Fairly large are the bony protuberances on the skull of Giraffidae and the horn-cores in Cavicornia. Absolutely large for a bird is also the bony knob on the upper bill of *Buceros* (see my fig. 15). Absolutely small are the bony knobs in a number of other birds and also the bony knobs under the horns in Rhinocerotidae.

The larger the weapons on the head – also in the absolute sense – the more important will be their influence on the architecture of the skull, in the first place by their presence as such, secondly by the strong development of the elements of the skull in the places where these weapons are attached to the skull and thirdly because other components of the skull from the place of attachment of the weapon towards the cervical vertebral column have changed in connection with the impact of the butting, which they must transfer from the weapon on the skull to the vertebral column.

In *Bos taurus* L. *e.g.* the fore head is very much thickened in connection with the way of fighting (MARINELLI, 1929, p. 131) (see my fig. 2 *h*). The sides of the skull also are strengthened at the place of attachment of powerful horns and antlers. This is one of the functions of the postorbital pillar (MARINELLI, 1933, p. 205). As already mentioned, the influence upon the architecture of the skull extends as far as the cervical vertebral column: in *Bos taurus* L. the base of the skull which receives the impact of the butting of the horns and transfers it to the cervical vertebral column, is strongly built. From a passage in STADTMÜLLER (1936, pp. 980/981) one might deduce that according to him not only the development of the molares, but also the development of the weapons on the head in Artiodactyla influences the size of the orbital and facial part of the lacrimale.

The relative size

Among the Pisces the relative size of the spikes, spines and thorns is very different. GREGORY (1933, p. 427) observes that the single backwardly-directed spike in *Holocentrus* (fig. 112), *Prionotus* (fig. 218), *Dactylopterus* (figs 222, 223), *Callionymus* (fig. 242) and *Gobiesox* (figs 249, 250) attains great size. In the introduction to this paragraph, however, we have seen that in the three genera last mentioned the spikes are not used as weapons. Whether and to what extent the spikes in the two first mentioned genera serve as weapons and also how matters stand in this respect with the spikes, spines and thorns to be mentioned below, is unknown to me. GREGORY mentions very large spines in *Bovichthys* (p. 358, fig. 240 C) and *Trachinus* (p. 363, fig. 243); large spikes in *Opsanus tau* (L.) (p. 386, fig. 263); prominent spikes in Scorpaenidae in general (p. 322) (see my fig. 79); strong spines in *Caracanthus* (*Micropus*) (p. 341), while those of *Platycephalus* (p. 330, fig. 211) are called small. The possession of very large spines, occurring in small numbers or even singly, is considered to be derived from a more primitive condition in which less prominent spikes were present in great numbers (p. 427). With the size of the spikes is connected the development of strengthening ribs on the skeletal element, from which the spikes project (GREGORY, 1933, p. 427, figs 114, 202, 298).

Also in a relative sense the horns of a number of † Ceratopsia are large (see my fig. 165). Relatively very large are the antlers with the bony pedicles in the Cervidae. In a relative sense the bony protuberances on the skull of the Giraffidae (see my fig. 150) and the horn-cores on the skull in Cavicornia (see my figs 2 *h*, 99, 112) are not very large. Relatively very large is the bony protuberance on the upper bill in *Buceros* (see my fig. 15). Bony knobs on the upper bill or on the skull of other Aves may be relatively rather large, but in other cases definitely small. Relatively very small are the bony knobs under the horns in the Rhinocerotidae (see my fig. 58).

With the relative size of the weapons on the head is, in Tetrapoda, also connected the relative size of strengthenings and thickenings of the components of the skull, which carry these weapons and which must transfer the impact of the butting to the cervical vertebral column. For examples we refer to the observations on this matter in the discussion of the absolute size.

c. The position

The spikes, spines and thorns in Pisces, which, however, as we have seen in the introduction to this paragraph, may be only partially regarded as weapons, are carried by several different elements of the skull. The largest spikes are found at the posterior corner or elbow of the praeoperculum (GREGORY, 1933, p. 427, see also pp. 322, 330, 332/333, 341, 367, 426) (see my figs 79, 115, 124, 146). But also on the operculum spines are often found (pp. 322, 332/333, 341, 356, 358, 360, 363, 386), sometimes also on the interoperculum (p. 341) and suboperculum (p. 367) (see my figs 75, 79, 124). In Scorpaenidae, however, prominent spikes occur also on the top of the skull, on the posterior borders of the posttemporal plates and in other species the whole head bristles with sharp spikes (p. 322) (see my figs 75, 79, 124). In Triglidae a spike occurs above the orbita, others on the skull-top behind the orbita (p. 341) (see my figs 117, 118). *Trichodon* has spikes on the lacrimale (p. 371).

In the later † Ceratopsia the unpaired horn stands on the nasalia and the paired horn on the postorbitalia (Versluys, 1936, p. 796) (see my fig. 165).

In Aves the protuberances on the upper bill and on the head itself are carried by several different elements of the skull (Marinelli, 1936, pp. 810/811) (see my fig. 15).

In Rhinocerotidae the bony knobs are situated on the nasale and frontale; in † Dinoceratidae they are carried by the maxillare and frontale, while *Giraffa camelopardalis* (L.) has also lateral horns on the parietale and occipitale (Stadtmüller, 1936, pp. 924, 926, 982) (see my figs 58, 150).

As the weapons on the skull can be situated on different elements of the skull, so different elements have been thickened and strengthened as carriers of the weapons on the skull and there are different ways in which elements between the carrying element and the cervical vertebral column, have been changed in their structure. So Marinelli (1929, p. 131) observes that in *Bos taurus* L., where the impect of the butting is transferred from the horns to the cervical vertebral column *via* the base of the skull, every angle in the axis, which might carry the risk of spraining ("Verrenkung"), has been avoided. So the base of the skull in *Bos taurus* L. lies in line and level with the cervical vertebral column in accordance with the hanging type of neck (see p. 381/382) (see my fig. 2 *h*). In *Equus caballus* L., in which the fore head is also directed forward, but not specialised for butting, the base of the skull has a quite different position; the neck of *Equus caballus* L. belongs to the carrying type (Marinelli, 1929, p. 132) (see my fig. 2 *j*).

d. Homology and non-homology

The differences in position of the weapons on the skull, which in several groups can be very considerable, may to a large extent be due to the fact that several morphologically very different formations are concerned. The spikes, spines and thorns of the Pisces are not homologous with the horn-cores of the Cavicornia, but even within a certain class these formations are not always homologous. I mention in this connection the spikes, spines and thorns of Pisces, which are situated in so many divergent places, and further the weapons on the head of the Mammalia, carried by different elements of the skull. The reverse can also be the case: non-homologous formations may be attached to the skull in the same place, *e.g.* the antlers of the Cervidae and the horn-cores of the Cavicornia.

67. NUCHAL AND NECK SHIELD AND PLATE

a. Introduction

In this paragraph we shall treat the backwardly freely projecting bony shields or plates on the skull, which can extend unto within the region of the neck.

Undoubtedly the function of the neck shield and neck plate is not a single and simple one. Concerning the Pisces GREGORY (1933, p. 441) remarks that for sluggish or partly sedentary fishes the protective value of a cranial shield would seem to be high, while in some of the Triglidae the cranial shield becomes heavy and seems to serve as ballast. In † Ceratopsia the neck shield has in addition to a protective function undoubtedly some importance in connection with the position of the centre of gravity of the whole body. The same applies to the huge crista on the occiput of † *Pteranodon*, which perhaps acts as a rudder too.

To the formations to be treated here belong among the Pisces the nuchal shield of the Siluroidei (Nematognathi), which partly consists of the posterior process of the supraoccipitale, but to which also contribute the expanded and coalesced bony supports of the first three rays of the dorsal fin (GREGORY, 1933, pp. 195, 441). This separate nuchal shield in the typical forms of the Siluroidei (Nematognathi) is often found in addition to a sort of cephalic shield, into which the skull roof is widened out and to which the broadened supraorbitale, dermosphenoticum, sphenoticum, pteroticum and posttemporal plates contribute (p. 195). Such a cranial or cephalic shield had developed quite independently in several groups of Pisces, such as in † Antiarcha (p. 100), certain families of Siluroidei (fig. 80), the Triglidae (figs 218–220) and in *Dactylopterus* (p. 441). In *Dactylopterus* the greatly enlarged roofing bones have grown backward over the neck and the plates above the shoulder girdle have been expanded into a huge neck shield, which is conjoined by immovable sutures with the expanded cranial roof (GREGORY, 1933, pp. 343, 441; fig. 223).

In this paragraph belongs also the neck shield which occurs in a number of † Ceratopsia (see my fig. 165) and the enormous crista on the occiput of † *Pteranodon*.

b. The size

The absolute size

The absolute size of the nuchal shield and of the cranial or cephalic shield, as far as it projects backwards as a neck shield, is always small, because the body size of the Pisces is small in an absolute sense.

The absolute size of the neck shield of the † Ceratopsia on the contrary is enormous, even when it is not strongly developed. In accordance with the varying degree of development of the neck shield in the † Ceratopsia, the absolute size of it is divergent too. The absolute size of the crista on the occiput of † *Pteranodon* is considerable.

The relative size

The relative size of the nuchal shield and the cranial or cephalic shield in *Dactylopterus* is very large; the relative size of the cranial or cephalic shield in other Pisces mentioned is much smaller.

The neck shield in † Ceratopsia is developed to a very varying degree and consequently the relative size may vary from small to huge (see my fig. 165). Very large is the relative size of the crista on the occiput of † *Pteranodon*.

c. The position

As the name already denotes, the neck shield is situated at the back border or back wall of the roof of the skull.

d. Homology and non-homology

When judging the size and the position we must bear in mind that not all formations treated here, are homologous. In the first place we mention as non-homologous the formations in Pisces and in † Ceratopsia and the crista on the occiput of

† *Pteranodon*. But also within the class of the Pisces the nuchal shield and the cranial or cephalic shield are morphologically different. The latter has been developed quite independently in several groups of fishes; so homology is not self evident here either and convergence occurs (GREGORY, 1933, pp. 196, 441).

68. CAVITIES AND GROOVES CONTAINING GLANDS OF THE HEAD

a. Introduction

This paragraph is concerned with a number of glands of the head in several Vertebrates, as the glandula intermaxillaris in recent Amphibia and other mucous glands in Amphibia and † Stegocephala, the lacrimal glands in Sauropsida and Mammalia, glands of the nose in Aves, maxillary dermal glands in certain Mammalia *etc.*

b. The connection between the size of the cavities and grooves containing glands of the head and the size of the glands themselves

The gland of the nose in Aves is contained in the fossae supraorbitales ("Supraorbitalgruben") in the frontale, but this gland need not be contained entirely in these grooves and it may be present though the grooves in the frontale are absent (MARINELLI, 1936, p. 824). Yet, according to STRESEMANN (1927, p. 51) the depth of the fossa supraorbitalis is determined by the degree of development of the gland of the nose.

From the above we may conclude that there may be a direct relation between the degree of development of the gland of the head and the size of the cavity or the depth of the groove in the skull, in which this gland is contained, but this need not always be the case. Further data concerning this matter would be desirable.

c. The size of the cavities and grooves containing glands of the head

Exact data on the size of these cavities and grooves are lacking in the literature consulted. Let it therefore suffice to collect here the data on the presence of such cavities or grooves, for the mere fact of their presence resp. absence has its influence upon the architecture of the skull.

The cavum praenasale of the Salientia contains the glandula intermaxillaris, while in the Caudata this gland is lodged in the cavum internasale *s.* intermaxillare, but this need not be the case (STADTMÜLLER, 1936, pp. 561, 635).

The fenestra internasalis (the so-called "Fazialgrube"), which occurs in some † Stegocephala and in recent Caudata, may be large; it is the entrance of the spatium internasale, a cavity in which a mucous gland is situated (STADTMÜLLER, 1936, pp. 598/599).

The preorbital or antorbital foramen in some † Stegocephala probably also will have lodged a mucous gland (STADTMÜLLER, 1936, p. 599).

In Aves the frontalia often have, near their borders, grooves for the glandulae supraorbitales (MARINELLI, 1936, p. 818). As we already mentioned in the introduction to this paragraph, the depth of these grooves is according to STRESEMANN (1927, p. 51) determined by the degree of development of the gland of the nose. This is important with respect to the architecture of the skull, because the bone at the bottom and the borders of these fossae supraorbitales may be extremely thin, so much so that this part of the frontale may even disappear altogether (MARINELLI, 1936, p. 824) (see my fig. 52).

The lacrimale in the Mammalia is more or less influenced in its structure by the lacrimal glands and this influence is in proportion with the degree of development of the lacrimal glands.

The groove on the facial surface of the maxillare in "Antilopinae" lodges a maxillary dermal gland (STADTMÜLLER, 1936, p. 981).

The Mesaxonia possess preorbital grooves containing dermal glands (STADTMÜLLER, 1936, p. 982).

d. The position of the cavities and grooves containing glands of the head

The mere names of the cavities and grooves and of the foramina giving access to the cavities, give so much information concerning their position, that a special discussion of this position in connection with the data quoted above from the literature consulted would only mean a repetition of the facts just mentioned.

e. Homology and non-homology

The differences in position of the different cavities and grooves containing glands of the head, are to a considerable extent due to the fact that several morphologically quite different glands are concerned and that accordingly the cavities and grooves in which they are situated are not homologous.

69. DENTIGEROUS PLATE

a. Introduction

The dentigerous plate is that part of the skull to which the teeth or in the highest Vertebrata the teeth and molares are attached. Consequently we do not include those parts of the dental area which in the lowest Pisces do not occupy parts of the skull, but are situated *e.g.* on the soft part of the floor of the lower jaw (GREGORY, 1933, pp. 127, 423).

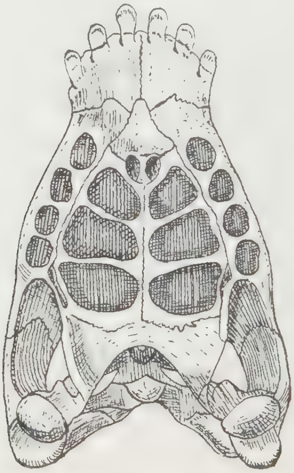

Fig. 166. *Placodus.* Skull seen in ventral view. After WILLISTON (1925), fig. 49 B on p. 59.

The dentigerous plate may consist of the following components: elements of the new upper jaw (praemaxillare and maxillare), elements of the new lower jaw (dentale and coronoid or spleniale; see GREGORY, 1933, p. 423), the old lower jaw (mandibula of the Elasmobranchii), elements of the old upper jaw (palatoquadratum of the Elasmobranchii; in the higher Vertebrata: palatinum, ento-, ecto- and metapterygoid), parts of the rest of the primary roof of the mouth (vomeres, parasphenoid) (see my fig. 166) and the pharyngeal surface of the hyoid arch and branchial arches (ceratohyale, glossohyale, second basibranchiale, fourth pharyngobranchiale, fifth ceratobranchiale, lower branchial elements) (GREGORY, 1933, pp. 423/424).

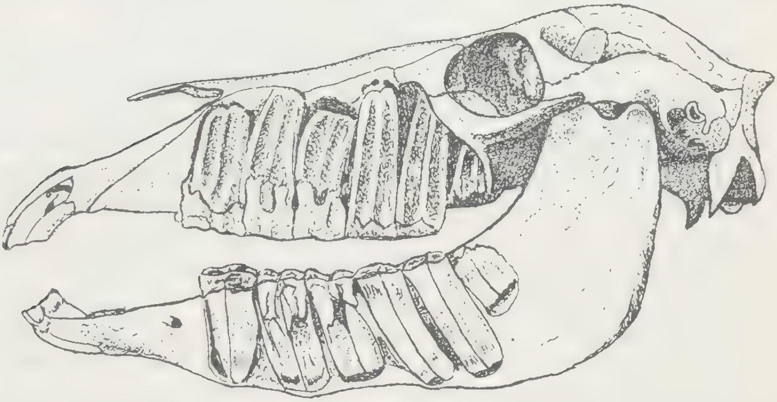

Fig. 167. *Equus caballus* L., $2^1/_2$ years old. Skull seen from the right side inverted. Sculptured to show the embedded parts of the teeth. After SISSON & GROSSMAN (1947), fig. 347 on p. 405.

Besides the length of these several components of the dentigerous plate, the development in breadth and thickness or height of the elements of the skull bearing these components of the dentition, is important and has a close connection with the degree of development of the dentition in those places (strength, breadth of the teeth, length of the roots of the teeth) (see my fig. 167). So this side of the problem must also be considered. As the development of the upper and lower jaw has already been treated in previous paragraphs, this will not be discussed here as such.

b. The size

Exact data concerning the size of the dentigerous plate, in an absolute as well as in a relative sense, are lacking.

The absolute as well as the relative size of the dentigerous plate, depends in the first place on the number of elements of the skull on which components of the dentigerous plate are situated (which depends on the taxonomic group) and secondly on the length of the dentigerous plate on each of these skull elements and on the breadth and thickness or height of each of these components, which in their turn are connected with the degree of development of the teeth and their roots, of the dentition in general (all this is related with the use of the teeth and the kind of food).

As to the number of skull elements bearing teeth, we can observe the following facts. In Elasmobranchii the dentigerous plate is constituted by palatoquadratum and mandibula (GREGORY, 1933, pp. 102/103) (see my figs 61, 130 *a*). In the higher Pisces, however, by new upper jaw, new lower jaw, primary upper jaw, elements of the rest of the primary roof of the mouth (vomeres, parasphenoid) and the pharyngeal surface of the hyoid and branchial arches (GREGORY, 1933, pp. 423/424) (see my figs 18, 19, 27, 28, 30, 40, 41, 42, 43, 50, 63, 65, 76, 77, 79, 81, 82, 83, 85, 86, 87, 88, 89, 91, 94, 95, 115, 116, 117, 118, 119, 120, 122, 123, 124, 125, 126, 127, 128, 129, 130, 143, 146). In Amphibia the dentigerous plate is situated on the new upper jaw and the new lower jaw, often also on vomeres and parasphenoid; in some Salientia it extends also on elements of the primary upper jaw (see my figs 20, 31, 96, 131). In Reptilia the dentigerous plate is found on the new upper jaw and the new lower jaw; in some Reptilia also on elements of the primary upper jaw (VERSLUYS, 1936, p. 802), rarely on the rest of the primary roof of the mouth (see my figs 9, 10, 12, 32, 44, 53, 55, 100, 101, 102, 103, 104, 105, 132, 135, 151, 163, 164, 165, 166). In Mammalia the dentigerous plate is restricted to the margins of the new upper jaw and the new lower jaw (see my figs 1, 2, 3, 5, 6, 7, 8, 26, 35, 37, 46, 47, 48, 49, 58, 60, 70, 71, 99, 108, 109, 110, 111, 112, 113, 134, 136, 137, 138, 139, 140, 141, 142, 144, 147, 148, 149, 150, 152, 153, 154, 155, 156 *a*, *b*, *c*, 157, 167, 168, 169, 170).

The length of the dentigerous plate on each of these components and also the development in breadth and thickness or height of each of these dentigerous skull elements depends on the use of the teeth and so on the kind of food; accordingly the dentigerous plate is long and strong in predaceous animals, whereas it may be very short and very weakly developed in animals taking very small food. In recent Aves it is lacking altogether.

The absolute size

The absolute size of the dentigerous plate and the absolute body size run parallel to a certain extent. Absolutely large animals have absolutely large jaws and the reverse. But this parallelism is interfered with by other factors: in the lower Vertebrata the dentigerous plate is situated not only on the margins of the jaws, but also on many other elements of the skull, and secondly within every large taxonomic group there are differences in the length of the dentigerous plate due to different use of the teeth and so to the kind of food.

For instance the absolute body size of the higher Pisces is small and accordingly the absolute length of the new upper jaw and new lower jaw is short. But the absolute size of the dentigerous plate is increased by the great number of skull elements bearing teeth, in addition to the margins of the jaws. Within the group of the higher Pisces several variations are found, due to different use of the teeth and so to the kind of food.

The divergence in length of the dentigerous plate on the new upper jaw and the new lower jaw is illustrated by the principle types of jaws, which GREGORY (1933, p. 423) distinguishes. He mentions the following five types and then points out a sixth one:

I. The normal type of jaws, occurring in all large taxonomic groups of Pisces, does not require a detailed discussion in relation to our problem. The small teeth occurring in this type do not impose any special demands on the skeletal elements to which they are attached (see my fig. 28).

II. The predaceous type of jaws, also occurring in all large taxonomic groups of Pisces. As a rule the emphasis falls on the teeth of the secondary jaws. The row of teeth will be long and as the teeth are usually large, the dentigerous skeleton will be strongly developed. As examples from several different large groups of Pisces GREGORY (1933, p. 423) mentions: † *Megalichthys* (Crossopterygii), † *Cheirolepis* († Palaeoniscoidei; see also figs 12 A, 283 A, 286 A) (see my figs 95, 143 *a*), *Protosphyraena* (Holostei), *Astronesthes* (Isospondyli), *Hydrocyon* (Ostariophysi; see also fig. 69) (see my fig. 86) and *Trichiurus* (Perciformes; see also figs 195, 291 D). Indeed in the more typical palaeozoic Crossopterygii in general, which are highly predaceous types, the rows of strong teeth on the large jaws are long; moreover there are a few very large tusks on the primary upper jaw and on the coronoid bones of the mandible (GREGORY, 1933, pp. 105/

107). This great length of the dentigerous plate on the new upper and lower jaw also holds good in the examples of a predaceous type of jaws to be mentioned below. According to GREGORY (1933, p. 423) in the predaceous Esocidae (see also p. 214, fig. 95 A) (see my fig. 30), Sphyraenidae (see also fig. 141), *Omosudis* (see also fig. 89) and other types also the teeth on the primary jaws and on the rest of the roof of the mouth are well developed, and thus also the inner upper jaw as well. In *Esox*, however, probably in connection with the above, the teeth on the new upper jaw are small (p. 214, fig. 95 A) (see my fig. 30); so here the rule which we mentioned in the beginning, *viz.* that the emphasis falls on the teeth of the secondary jaw, does not hold good in this case. The presence of stout teeth on the palate in *Lepisosteus* and *Osteoglossum* necessitates extra bracing of the palate (GREGORY, 1933, p. 423, see also pp. 164, 166, figs 24, 57) (see my figs 65, 116). In *Lycodontis* on the other hand the palatopterygoid tract degenerates, as the maxilla and vomer bear the principal teeth (p. 423, fig. 82 B) (see my fig. 119).

III. The small-mouthed nibbling type of jaws, which also occurs in nearly all large taxonomic groups of Pisces. In this type the new upper and lower jaw are short and, accordingly, so is the part of the dentigerous plate attached to them. As examples GREGORY (1933, p. 423) mentions: † *Mesolepis* († Palaeoniscoidei), *Mesodon* (Holostei), *Distichodus* (Ostariophysi; see also fig. 71) and *Chaetodon* (Perciformes; see also figs 155, 291 B). In *Dorosoma* (*Chatoessus*), which GREGORY (1933, p. 423, see also p. 146, fig. 39) (see my fig. 29) cites as an example from the Isospondyli, teeth are lacking altogether.

IV. The crushing type of jaws, also occurring in many of the large taxonomic groups of Pisces. The dentigerous plate is short, but praemaxillare and dentale are massive and the bracing bones of the jaws are very strongly built (GREGORY, 1933, p. 423, see also pp. 376/377). As examples GREGORY (1933, p. 423) mentions: *Mylacanthus* (Crossopterygii), † *Cheirodus* († Palaeoniscoidei; fig. 15 A), *Lepidotus* (Holostei) and *Archosargus* (Perciformes; figs 123, 291) (see my fig. 89). In Dipnoi, too, adaptations for crushing hard substances occur and in connection with this we find a firm foundation for the dental plates on the roof of the mouth. In the oldest known Dipneusta there were no teeth on the praemaxillare, maxillare and dentale, but there were one pair of clusters on the roof of the mouth, a pair of small patches on the vomerine region and a pair of clusters on the splenialia (GREGORY, 1933, pp. 104, 105) (see my fig. 130 *b*).

V. The needle-gar type of jaws, likewise occurring in a number of large taxonomic groups of Pisces. In this type the new upper and lower jaws are very long; they are with or without teeth, in other words the dentigerous plate on the new jaws is in an absolute sense either long or altogether lacking. Among the examples mentioned by GREGORY (1933, p. 423) the jaws of † *Saurichthys* († Palaeoniscoidei) are, according to the picture (fig. 16), toothless, whereas *Tylosurus* (Perciformes; see figs 99, 289 A, 291 E) (see my fig. 94) has a long row of teeth. Whether *Aspidorhynchus* (Holostei) had teeth in the new upper and lower jaws or not, cannot be concluded from GREGORY's study (1933).

VI. The protrusile type of jaws, which occurs in a few large taxonomic groups of Pisces. GREGORY (1933, p. 423), who adds this type of jaws to his list, calls it edentulous. Such a toothless protractile mouth is found in *Phractolaemus* (p. 424). In *Percopsis guttatus* Ag., however, the protrusile mouth is bordered by minute teeth (p. 232). Some protrusile mouths have lost their teeth, others have not (pp. 423, 424).

This edentulous condition applies to the new upper and lower jaws and the same occurred already in the types discussed previously (see *Dorosoma* (*Chatoessus*) and † *Saurichthys*).

In *Polyodon*, however, the teeth are completely absent (GREGORY, 1933, p. 424, fig. 17), not only from the new upper and lower jaws, but also from the other parts of the dentigerous plate. GREGORY (1933, p. 424) follows this up with the observation that in *Cetorhinus*, *Rhineodon* and *Mobula* the teeth are more or less reduced, the meaning of which is not quite clear, because reduction may mean many different things (reduction in size, in number on each component of the dentigerous plate and reduction in the number of components of the dentigerous plate).

We shall follow up these data concerning the lack of teeth on the new upper and lower jaws in general and especially in the protrusile type of jaws, in some other cases.

In *Gonorhynchus*, too, teeth are absent from the new upper and lower jaws and occur only on the second basibranchiale and on the entopterygoid; these two rows of teeth constitute the entire dentition of the animal (GREGORY, 1933, p. 177) (see my fig. 64). It is possible in † *Charitosomus* that the dentition was the same as in *Gonorhynchus* (p. 179).

In Cyprinidae, too, teeth are lacking on the new upper and lower jaws, but the absence of teeth on the jaws is more than compensated by the presence of the teeth on the fifth ceratobranchialia (p. 193).

In Mormyridae there are no teeth on the maxillare, vomer, palatinum and pterygoid; only the praemaxillare and the dentale are provided with teeth (p. 171).

In † *Notogoneus* there are no pterygoid and lingual teeth (p. 179). In *Pogonias* the palate is toothless, but there are teeth on the jaws and there are also lower pharyngeal teeth, stout, pebble-like crushing teeth which parallel those in the jaws of sparids (p. 252).

It is impossible to give more than these occasional observations on the absence of certain components of the dentigerous plate in Pisces. This list is incomplete and the literature consulted gives no information on the lengths of the parts of the dentigerous plate on the primary upper jaw, on the rest of the roof of the mouth (on vomeres and parasphenoid) and on the hyoid and branchial arches.

Some occasional observations on the development in breadth and thickness or height and on the attachment of the elements of the skull bearing these teeth, may follow.

In Clupeoidea with heavy pharyngeal dentition the supporting parts of the branchial apparatus are braced to the base of the cranium (Gregory, 1933, p. 425). The rod-like character of the metapterygoid in *Gonorhynchus* is comprehensible when the movements of the teeth on the dorsal surface of the second basibranchiale, with respect to the teeth on the entopterygoidea, are taken into account (Gregory, 1933, pp. 177, 423). † *Charitosomus* is perhaps similar to *Gonorhynchus* in this respect (p. 179). In Scaridae the fused lower pharyngealia, which bear pharyngeal teeth, fit into grooves on the inner side of the cleithra (pp. 424, 425).

So far on the absolute size of the dentigerous plate in Pisces.

In Amphibia the skull is generally small in an absolute sense and consequently the dentigerous plate is small too, though it may extend very far backward in some cases on the new upper and lower jaw and moreover other parts of it are situated on the primary upper jaw and on the rest of the roof of the mouth (vomeres, parasphenoid). As the teeth are slightly developed on all these parts, no special demands are made on the attachment of the dentigerous elements of the skull, which is, consequently, slightly developed (see my figs 20, 31, 96, 131).

Among the Reptilia sometimes skulls occur, which are very large in an absolute sense, in which cases the dentigerous plate is also absolutely large, owing to the length of the new upper and lower jaw. Only in a very few cases is the dentigerous plate extended by the presence of additional parts on elements of the primary upper jaw and on the rest of the roof of the mouth (see my fig. 166). However, there are also Reptilia with an absolutely small skull and accordingly an absolutely small dentigerous plate. The attachment of the new jaws has been discussed previously and the attachment of the rarely occurring other components of the dentigerous plate does not give occasion to special remarks. Finally there are toothless Reptilia, *e.g.* the Testudinides in which the absolute size of the dentigerous plate is, accordingly, nihil (see my figs 11, 45, 132, 160).

The Aves, at least the recent ones, are also toothless, so the absolute size of the dentigerous plate is, in this case nihil, too (see my fig. 133).

In Mammalia the dentigerous plate is limited to the margins of the new upper and lower jaw, so for that reason the dentigerous plate is small in an absolute sense. But the margins of the jaws themselves are in many cases absolutely very large, because there are among the Mammalia many species with an absolutely large skull. However there are also numerous small Mammalia with an absolutely small dentigerous plate. Finally the dentigerous plate is absent in Monotremata, in a number of Edentata and in Mystacoceti (see my figs 2 *d*, *e*, 107, 134 *a*, *b*, *i*, *j*, *m*, *v*). The attachment of the dentigerous plate has been previously discussed, when the attachment of the new upper jaw and the lower jaw was discussed.

The relative size

Considering the relative size of the dentigerous plate, our conclusions will be quite different from those on the absolute size of the dentigerous plate. In the lower Vertebrata, such as Pisces and Amphibia, which are generally small in an absolute sense, the relative length of the dentigerous plate is extremely large owing to the additional parts of the dentigerous plate on other components of the skull besides the new upper and lower jaw. In Mammalia, which are absolutely large the dentigerous plate, though large in an absolute sense, is relatively small, because it is limited to the margins of the new upper and lower jaws and moreover the upper jaw does not extend very far backward because of the more rostral position of the jaw joint.

Concerning the relative length of the dentigerous plate in the higher Pisces we may point out that in the six types of jaws mentioned above, this relative length on the new jaws is rather divergent. In the predaceous type of jaws the length of the dentigerous plate on the new jaws will be relatively longer than in the normal type of jaws and much longer than in the small-mouthed nibbling type of jaws and also longer than in the crushing and the protrusile types of jaws. However the needle-gar type of jaws surpasses the predaceous type considerably with regard to the relative length of the dentigerous plate. Within some of these types edentulous new jaws occur as we have seen; it goes without saying that the relative length of the dentigerous plate on the new jaws is also nihil in those cases. Within each of these types, however, differences in the relative length of the dentigerous plate on the new jaws occur. *E.g.* within the predaceous type of jaws the dentigerous plate on the new jaws of *Hydrocyon* (GREGORY, 1933, fig. 69) (see my fig. 86) is relatively much shorter than in † *Cheirolepis* (figs 12 A, 283 A, 286 A) (see my figs 95, 143 *a*), *Lepisosteus* (fig. 24) (see my fig. 65), *Osteoglossum* (fig. 57) (see my fig. 116) and *Lycodontis* (fig. 82 B) (see my fig. 119). But these data concerning the relative length of the dentigerous plate on the new jaws do not give any information on the relative length of the entire dentigerous plate, but the literature consulted does not furnish sufficient data on the presence resp. absence of the other components of the dentigerous plate and on their relative lengths, to give us an insight in the relative length of the whole dentigerous plate.

In Amphibia the relative length of the dentigerous plate is considerable, because the dentigerous plate on the new jaws extends very far backwards, while in certain cases the relative length is increased again by components of the dentigerous plate on the primary upper jaw and on the rest of the roof of the mouth.

In Reptilia the relative length of the dentigerous plate is only in a few cases increased by components of the dentigerous plate on elements of the skull other than the new jaws; the relative length of the dentigerous plate may nevertheless be considerable, *viz.* in case the row of teeth extends very far caudalwards to within a short distance of the joint of the jaw, which is situated very far backwards. In the edentulous Testudinides the relative length of the dentigerous plate is nihil.

In recent Aves, too, the relative length of the dentigerous plate is nihil.

In Mammalia the relative length of the dentigerous plate is not very considerable, because there are no components of the dentigerous plate other than on the margins of the new jaws and because the joint of the jaw is situated rather far rostralwards. In Monotremata, in the edentulous Edentata and in Mystacoceti the relative length of the dentigerous plate is nihil. For the rest this relative length varies very much: in *Homo* it is rather short; in Odontoceti it may be very large [1]).

c. The position

We shall discuss the position of the dentigerous plate, arranged according to the several components, thus we shall treat separately the position of the dentigerous plate on the new upper jaw, on the new lower jaw, on the old lower jaw, on the elements of the old upper jaw, on the rest of the roof of the mouth and on the hyoid and branchial arches.

When discussing the position of the dentigerous plate on the new upper jaw, the position with regard to the orbita is especially important and the position of the caudal part in relation to the medial and lateral elements of the skull in the corresponding place.

The position of the dentigerous plate on the new upper jaw with regard to the orbita is very important in connection with the attachment of the caudal end of the new upper jaw, as we have seen in the discussion of this attachment.

As to the position of the dentigerous plate on the new upper jaw with regard to the orbita in the higher Pisces, we may refer to the discussion of the position of the new upper jaw itself with regard to the orbita. Otherwise we should keep repeating all these data, while they can only partially contribute to the answer to our problem, because the relation between the caudal border of the new upper jaw and that of its dentigerous plate has not been described with sufficient exactness in the higher Pisces.

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[1]) See: W. K. Gregory and M. Hellman (1940). The upper dental arch of Plesianthropus transvaalensis Broom, and its relations to other parts of the skull. Amer. J. phys. Anthrop., **26**, pp. 211—224. (Postwar addition in the manuscript)

In the Reptilia investigated by MARINELLI (1929, p. 135) the row of teeth extends to below the orbita in *Sphenodon* (*Hatteria*), *Iguana* and *Hydrosaurus* (*Lophura*); in *Varanus*, however, it ends on the level of the rostral border of the orbita (see my fig. 151).

In the Mammalia investigated by MARINELLI (1933, pp. 206, 215) the row of molares extends backwards to approximately halfway under the orbita in *Giraffa camelopardalis* (L.) (see my fig. 150); in *Okapia* and in fossil Giraffidae, as † *Helladotherium*, even to below the level of the caudal border of the orbita, while in *Equus caballus* L. (see my figs 149, 167) the orbita is situated behind the row of molares, which is connected with the general extension and the forward shifting of the maxillary part of the skull.

The position of the caudal part of the dentigerous plate on the new upper jaw with regard to lateral and median parts of the skull on the corresponding level is rather divergent in Mammalia. According to MARINELLI (1929, p. 136) the caudal part of the row of molares in Carnivora diverges lateralwards (see my fig. 153), whereas in herbivorous Mammalia the row of molares curves on the contrary medialwards (see my figs 147, 152, 168, 169). This is connected with the fact that the Carnivora when biting, use the hinder molares as a scissor-like mechanism to break the food ("Brechschere"); the most caudal molares are situated on the root of the temporal arch and – following its outline – diverge laterally. In herbivorous Mammalia it is not the musculus masseter, but the musculus pterygoideus, which acts on this caudal part of the row of molares. These caudal molares in herbivorous Mammalia are not situated on the temporal arch, but under the high middle part of the skull. In *Canis familiaris* L., in which the most caudal molares possess a broad grinding surface, they are situated more medially under the firm lateral wall of the skull, which acts as an inner buttress ("innere Unterstützungswand"), which is situated more medialwards than in true Carnivores (MARINELLI, 1929, p. 136). In a few cases the row of molares diverges in the rostral direction (see my fig. 170).

The position of the dentigerous plate on the new lower jaw is determined by the position of the new lower jaw itself, because the row of teeth is attached to the margin of the new lower jaw.

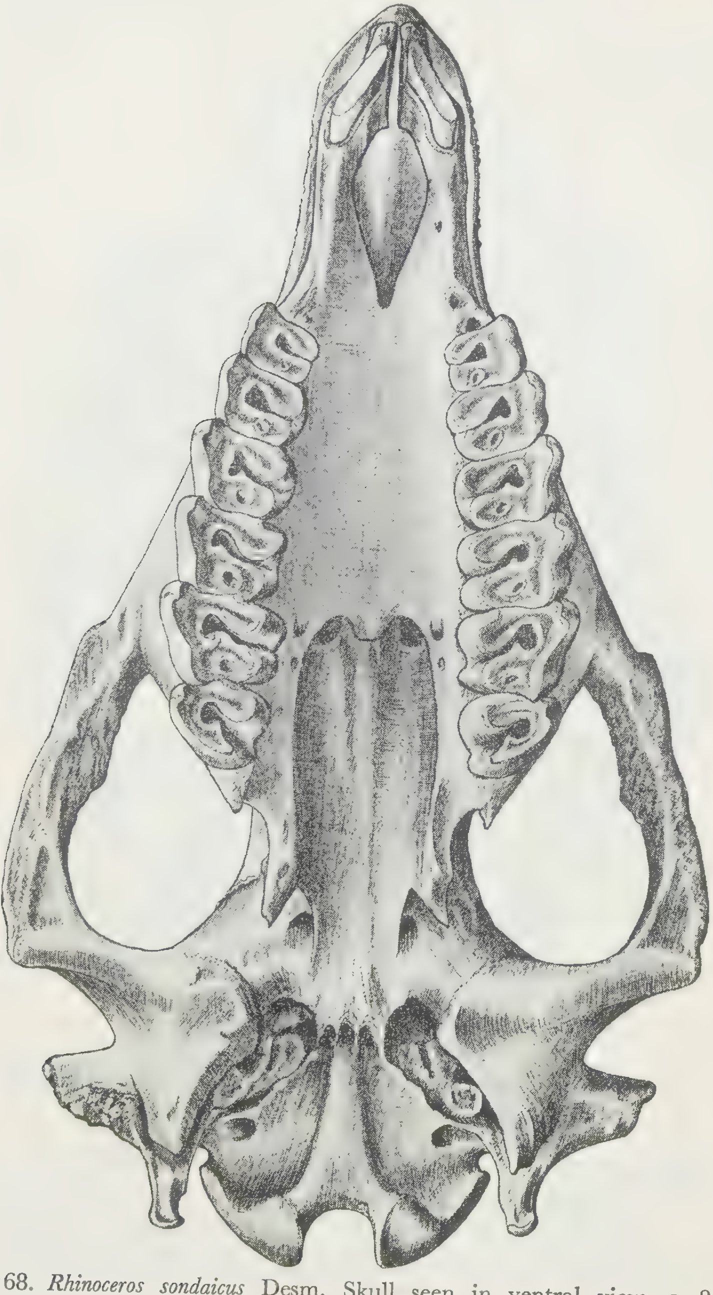

Fig. 168. *Rhinoceros sondaicus* Desm. Skull seen in ventral view. 0.28×
Original drawing by Mrs M. Idenburg in the
collection of dr K. W. Dammerman.

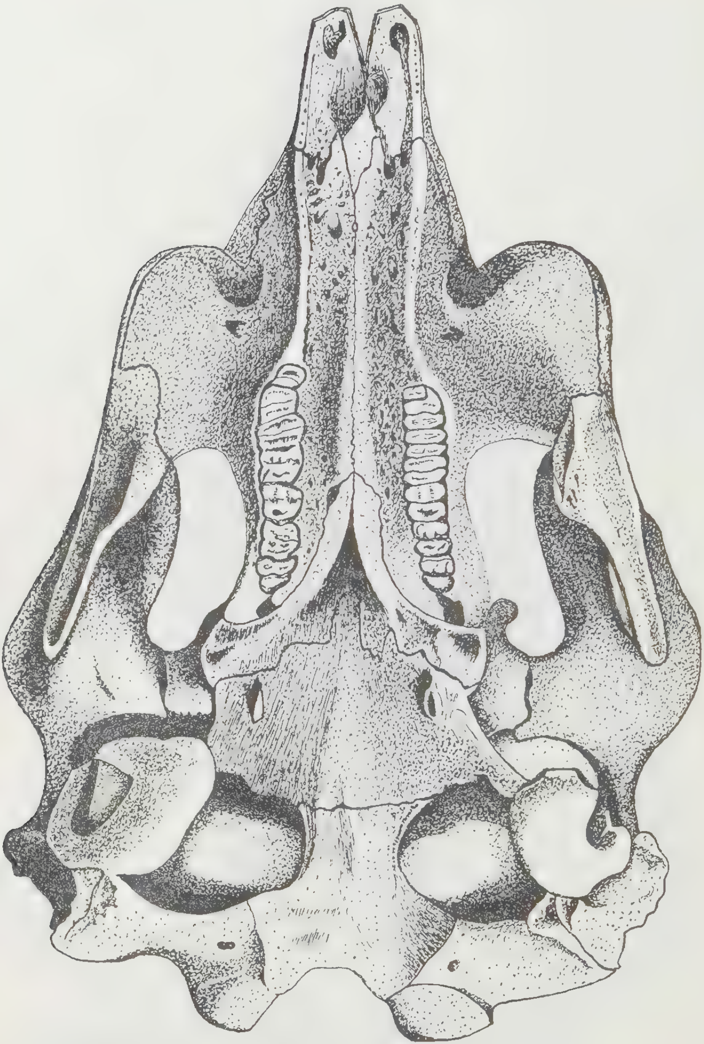

Fig. 169. *Trichechus latirostris* (Harl.) (*Manatus latirostris*). Skull seen in ventral view. After WEBER (1927), II, fig. 313 on p. 483.

The position of the dentigerous plate on the new lower jaw is also determined by the position of the dentigerous plate on the new upper jaw, because generally the rows of teeth in upper and lower jaw will fit together when the mouth is closed (see my fig. 141). When the mouth is opened this position is changed.

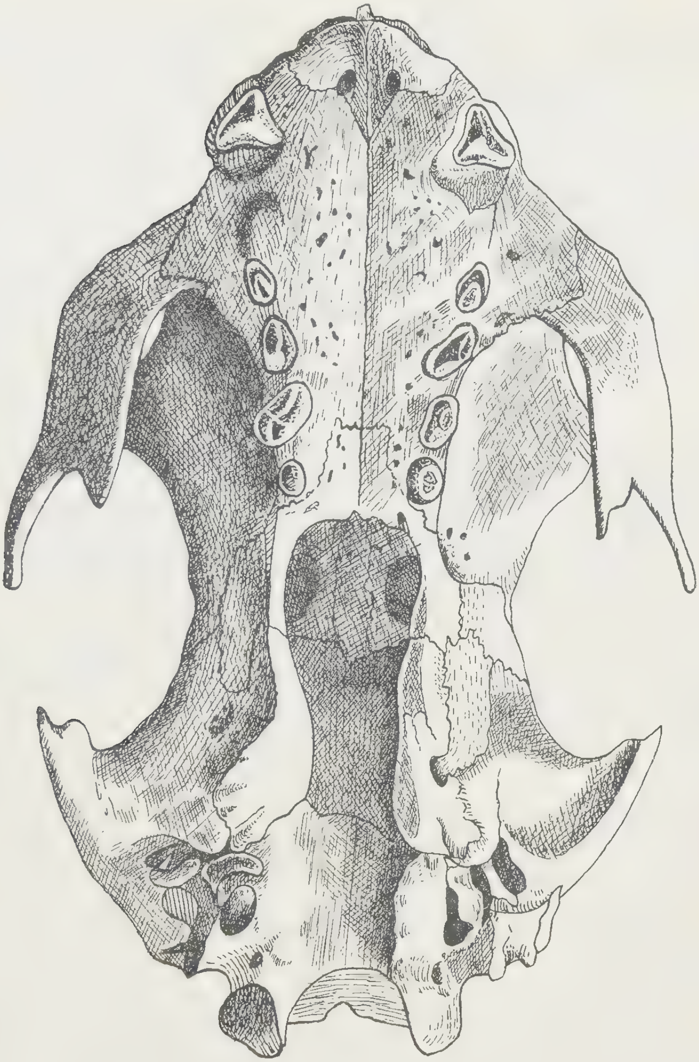

Fig. 170. *Choloepus.* Skull seen in ventral view. After WEBER (1927), II, fig. 117 on p. 194.

In Elasmobranchii the dentigerous plate lies on the old lower jaw and old upper jaw; their position is determined by that of mandibula and palatoquadratum itself (see my fig. 61).

The dentigerous plate on the roof of the mouth is situated partly on elements of the primary upper jaw and partly on the vomeres and the parasphenoid, which means between the right and left new upper jaw on the primary palate, the position of which will be discussed afterwards (see my figs 12, 18, 19, 104, 105, 146, 166).

The position of the part of the dentigerous plate which is situated on the pharyngeal surface of the hyoid and branchial arches, changes with the movements of the hyal and branchial skeleton. We shall treat the situations, occurring in the higher Pisces, in accordance with the way in which the lower pharyngeal teeth are opposed to the more dorsally situated teeth. The literature consulted mentions the fact that the lower pharyngeal teeth are situated opposite the teeth on the roof of the mouth, especially opposite those on the entopterygoid, in other cases opposite teeth on the parasphenoid and in still other cases the lower pharyngeal teeth lie opposite the basioccipitale and finally they can also be situated opposite upper pharyngeal teeth.

The teeth on the tongue (glossohyale and adjacent parts) oppose teeth on the roof of the mouth in the cretaceous and later Elopidae, Albulidae and related families (GREGORY, 1933, p. 423).

Teeth on the dorsal surface of the second basibranchiale engage with teeth on the entopterygoidea in *Gonorhynchus* (GREGORY, 1933, pp. 177, 423). In † *Charitosomus* the situation is probably the same as in *Gonorhynchus* (p. 179).

Teeth on the basihyale, glossohyale and basibranchiale and similar lingual teeth oppose teeth on the parasphenoid and other bones on the base of the cranium in many fossil and recent Osteoglossidae (GREGORY, 1933, p. 166).

In *Hyodon* the teeth on the tongue and floor of the mouth are situated opposite teeth on the parasphenoid (GREGORY, 1933, pp. 167/168).

The pharyngeal teeth on the enlarged fifth ceratobranchialia or lower pharyngealia oppose a horny pad that rests on a bony projection from the basioccipitale in the Cyprinidae and allied other Eventognathi (GREGORY, 1933, pp. 193, 223, 424, 439).

The situation that the lower pharyngeal teeth oppose the teeth on the upper pharyngealia occurs in many taxonomic groups of higher Pisces. In Microcyprini the teeth on the ceratobranchialia oppose the teeth on the upper pharyngealia (GREGORY, 1933, p. 424, see also p. 219). In Synentognathi, as *e.g.* *Tylosurus*, the teeth on the lower pharyngealia also may be opposed to those on the upper pharyngealia (pp. 221, 223, 424). We observe the same in Pomacentridae (pp. 255, 424), Cichlidae (pp. 254/255, 424), Chaetodontidae (p. 424), Embiotocidae (p. 424) and in Labridae (pp. 223, 256, 424). Concerning the Labridae mention is made of the fact that there is a pharyngeal mill as in Scaridae. In Scaridae the pharyngeal mill is the most elaborate part of the dental apparatus; the very powerful upper pharyngeal teeth lie on a sliding plate which finds a pedestal in the parasphenoid (GREGORY, 1933, pp. 424, 439, fig. 134). In *Opsanus tau* (L.) too, we find teeth on the upper and lower pharyngeal bones (p. 383).

d. Homology and non-homology

The differences in size and position of the dentigerous plate are to a considerable extent caused by the fact that the dentigerous plate in several groups does not consist of the same components, in other words, is not strictly homologous. The dentigerous plate which is situated on the primary upper and the primary lower jaw only, is quite different from the dentigerous plate attached to the margins of the new upper and the new lower jaw. And the components which may occur in addition to them on vomer and parasphenoid and on the hyoid and branchial arches, are different formations again.

70. PALATE

a. Introduction

In many cases the function of the palate is, no doubt, not a single or a simple one. We shall here consider the function of the palate only as the roof of the first part of the digestive tract, thus showing relations to the kind of food, the way of cutting up the food, in a number of cases also the way to separate the alimentary passage from the respiratory one. The palate, however, has also a function in attaching the new upper jaw to the skull, in kinesis and in bearing part of the dentigerous plate.

In the discussion of the palate we must distinguish two situations: 1° there is only a primary palate; 2° the primary palate is ventrally partly covered by a secondary palate.

In those taxonomic groups in which a secondary palate is present, the part of the primary palate which lies dorsally of it, has no actual function as a roof of the mouth cavity. To determine the size and position of this part of the primary palate, which has no true palatal function, we must know the position and extent of the palatum durum, but also of the secondary palatum molle. In the case of recent Loricata the knowledge of the palatum durum is sufficient in relation to this point; in that of the Serpentes the knowledge of the palatum molle suffices, but in the case of Testudinides and Mammalia palatum durum as well as palatum molle must be known.

b. The size

Exact data on the absolute as well as on the relative size of the palate are lacking.

In those Pisces, Amphibia and Reptilia in which the new upper jaw is situated at the extreme rostral and lateral borders of the skull and in which moreover the jaw joint lies at the caudolateral angle of the skull, while there is no secondary palate, the (primary) palate consists of the entire ventral surface of the skull, within the inner border of the row of the teeth (see my figs 12, 20, 97 *b*, 104, 105, 145 *d*, 166).

In those Pisces, Amphibia and Reptilia differing from the ones just mentioned only in the more rostral position of the jaw joint, the right and left caudolateral corners of the ventral surface of the skull do not contribute to the palate. In those cases the palate consists of the entire ventral surface of the skull in front of the line joining the right and left joints of the jaw, in so far as it lies within the inner border of the row of the teeth, and also of the medial part of the ventral surface of the skull caudally of this line (see my figs 145 *a*, *b*, *c*). In Aves, in which the joint of the jaw is always situated relatively far rostralwards, owing to the strong development of the brain in a caudal direction, the same situation occurs (see my fig. 171).

A third group of cases is constituted by those Reptilia in which the new upper jaw is also situated at the extreme rostral and lateral borders of the skull and in which the jaw joint is likewise situated at the caudolateral corner of the skull, but in which a secondary palate is present, either entirely skeletal, or entirely soft or partly skeletal and partly soft; this is the case respectively in Loricata, Serpentes and Testudinides. In these cases the palate is likewise constituted by the entire ventral surface of the skull, in so far as it lies within the inner border of the row of the teeth, but part of it is a primary palate and part of it is a secondary palate. If we want to know the share of both palates in the entire palate, we must also determine the size and the position of the soft palate, but this cannot be seen in the dried skull. Only in recent Loricata the secondary palate consists entirely of a palatum durum (see my fig. 10). The conditions found in recent Loricata show that there is a marked difference in extent and position between the rostral and the caudal part of the secondary palate. For the caudal part of the palatum durum in recent Loricata does not border on the ventrolateral edge of the secondary roof of the skull, but remains at a marked distance from it, separated from it by the posterior palatine opening. Whether and to what extent this relative narrowing of the caudal part of the secondary palatum durum in recent Loricata is related to one of the biological significances of the secondary palate (separation of the respiratory and alimentary passages; kind of food; way of cutting up the food; see VERSLUYS, 1936, p. 738) I do not know. In Testudinides the palate, at least the palatum durum, extends along its entire length over the full breadth of the ventral surface of the skull (within the inner border of the row of the teeth) in the corresponding place (see my fig. 11).

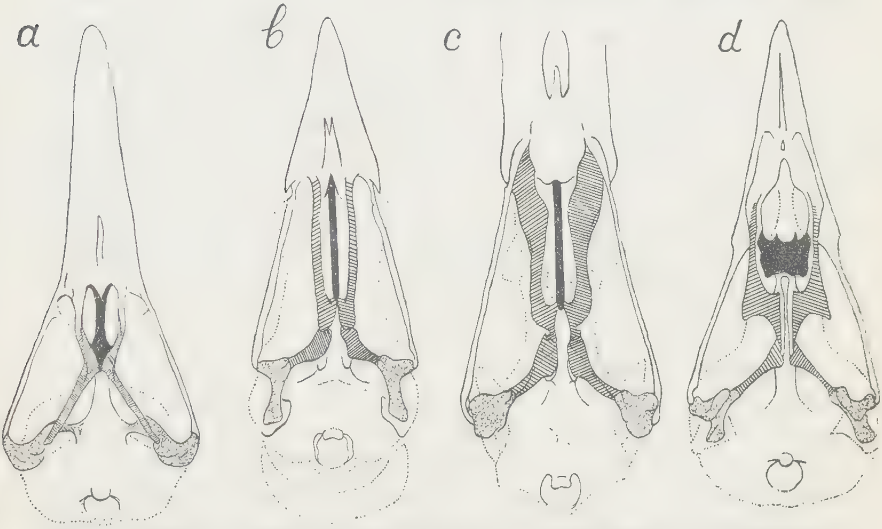

Fig. 171. Skulls of Aves, seen in ventral view. *a. Rhynchotus*; *b. Megacephalon*; *c. Cygnus*; *d. Corvus*. After PORTMANN (1950), fig. 82 on p. 105.

In a fourth group we may rubricate those cases in which the new upper jaw is also situated at the extreme rostral and lateral borders of the skull, but in which a secondary palate is present and the joint of the jaw lies more rostrally. This situation is found in Mammalia (see my figs 107 *c*, 110 *c*, 147, 152, 153, 156 *c*, 168, 169, 170) and also in a few Reptilia. In front of the line connecting the right and left joints of the jaw, the entire ventral surface of the skull, within the inner border of the row of the teeth, constitutes the palate; caudally from this line only the median part of the ventral surface of the skull belongs to the palate. If we want to determine the part which the primary palate and that which the secondary palate contributes in the formation of the entire palate, we must also know the size and position of the palatum molle, which cannot be seen in the dried skull. In Mammalia, however, the palatum durum extends along its entire length over the full breadth of the ventral surface of the skull in the corresponding place.

The absolute size

Exact data on the absolute size of the palate and also on the part which primary and secondary palate contribute to the surface of the entire palate, are lacking.

So we can only point out the parallelism which generally exists between the size of the skull and consequently of the animal, and the size of the palate in that sense, that absolutely small animals have an absolutely small palate and absolutely large animals a large one. We mention *e.g.* a small species among the Sauria or among the Rodentia, compared to a large *Crocodylus* or an *Elephas*.

The relative size

In determining more exactly the relative size of the palate, we must bear in mind that the size of the palate is expressed in square measure and consequently when the volume of the skulls is the same, it will be larger in low skulls (whether they are longer or broader) than in high skulls.

The relative size of the palate will to a considerable extent depend on the position of the jaw joint, because only in front of the line connecting the joints of the jaw the palate is constituted by the entire ventral surface of the skull (in so far as it lies within the inner border of the row of the teeth), while caudally of this line only the median part of the ventral side of the skull belongs to the palate. Consequently in an amphibian with its flat and broad skull with the joint of the jaw situated in the caudolateral angle, the palate will be relatively very large, whereas in a fish with a long snout and short jaws, the palate will be relatively very small.

As to determining the part which the secondary palate contributes to the relative size of the entire palate, we must limit ourselves to a few stray observations on the relative size of the palatum durum.

In Testudinides the palatum durum is small in a relative sense, in recent Loricata it is relatively large, at least very long, which is accompanied by a relative narrowing in the caudal part of the secondary palatum durum.

In Mammalia the palatum durum is generally large in a relative sense. In Mammalia a lengthening of the palatum durum is correlated with a reduction of the dentition (WEBER, 1927 I, p. 266). In Rodentia the whole hard palate is so short that the choanae are on a level with the last premolar (KINGSLEY, 1925, p. 198; STADTMÜLLER, 1936, p. 934). In some Rodentia the secondary palate is very narrow, owing to the position of the molares (STADTMÜLLER, 1936, p. 974).

A question of relative size of the palate in relation to that of the cerebral capsule is probably discussed by DUBOIS. This is the case, if the size of the skeletal palate has something to do with the size of the "palatal area" 1), which DUBOIS (1921, p. 990; 1922 a, p. 1274) mentions in relation to the size of the jaws. DUBOIS discussing the relation between the capacity of the upper part of the skull or calvaria with that of the entire cerebral capsule, draws attention to the influence of the height of the cerebral

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1) DUBOIS does not tell what is meant by "palatal area". A. KEITH, The Antiquity of Man (1st edition, 4th impression, 1920, pp. 97, 151/152, 328; 2nd edition, 1925, vol. I, pp. 101, 102, 147, 215, vol. II, pp. 526, 527, 659) gives as a definition of the palatal area "being the space bounded by the outer margins of the crowns of the teeth. The hinder border of the area is demarcated by a line joining the posterior margin of the last or third molar teeth"; discussing the whole area of the palate he says "all that lies inside the outer margin of the teeth, is directly concerned in mastication and the total area of the palate may therefore be accepted as the degree to which the apparatus of mastication has been developed", "the area of the palate may be taken as an index of the extent to which the masticatory system is developed".

capsule. In this respect there is a distinct difference whether the upper part of the skull is flattened (platycephalic) or high-vaulted. Between nearly related animals skulls with a flattened upper part of the skull will have a larger under part and larger jaws than skulls with a high-vaulted upper part. DUBOIS mentions that in *Symphalangus syndactylus* (Desm.) the ration capacity (that is the entire volume of the cerebral capsule): "palatal area" is 6.7 : 1, whereas in *Hylobates lar leuciscus* Geoffroy this ratio is 9.5 : 1. No doubt the volume of the cerebral capsule is taken in cm^3 and the surface of the palate in cm^2.

c. The position

When discussing the size of the palate we have rubricated the types of palates in four classes of cases, from which many consequences can be drawn concerning the position of the palate with regard to the ventral side of the skull and also general remarks have been made on the position of the secondary palate with regard to the primary palate. We may refer to this discussion in order to avoid repetitions.

d. Homology and non-homology

In judging the differences in size and position of the palate and its components, we must bear in mind that part of these differences are due to non-homology or incomplete homology. The primary palate is morphologically different from the secondary palate. The entirely hard, skeletal secondary palate of recent Loricata is not completely homologous with the secondary palate of the Testudinides and the Mammalia, which is only partly skeletal and hard.

71. THE PARASPHENOID IN ITS AXIS FUNCTION

a. Introduction

In Pisces one of the functions of the parasphenoid is to constitute a firm axis for the skull (MARINELLI, 1936, p. 229). The junction between the preorbital and the postorbital part of the skull is very weak in these tropidobasic skulls with very large orbitae. Rarely both parts are rather loose and movable relatively to each other, as in Crossopterygii, in which the parasphenoid accordingly does not extend very far rostralwards (HOLMGREN &

Stensiö, 1936, p. 363). Generally, however, this weak junction is strengthened by the parasphenoid and by the interorbital bridge, which will be discussed presently (see my figs 18, 19, 64, 83, 85, 114, 115, 116, 143*c*, 146). The demand for adequate firmness of the junction between the preorbital and the postorbital part of the skull results from two facts, firstly that the snout in Pisces acts as a bow (Marinelli, 1936, p. 229) and secondly that the pressure exercised by the teeth which in Pisces are sometimes strong in the preorbital part of the skull only, must be transferred to the postorbital part of the skull, to which the masticatory muscles are attached. Evidently the bow function of the preorbital part of the skull prevails, for in tropidobasic Amniota, in which the head does not act as a bow, the parasphenoid does not fulfil this axis function for the connection of the pre- and postorbital parts of the skull, as it is too narrow and too short for this. By this shortness and narrowness one of the conditions is fulfilled for the possibility of kinesis in the tropidobasic skull of the Amniota (Marinelli, 1936, p. 230).

For the subject of this paragraph it is important that in Pisces the parasphenoid ties the ethmo-vomerine block to the base of the brain case (Gregory, 1933, p. 435). Besides the parasphenoid in Pisces has other functions still, *e.g.* it forms the roof of the mouth and the floor of the interorbital septum, gives off dorsolateral wings or struts, which often form a secondary anterior wall of the brain case proper, affords attachment to a muscle and forms the floor of the myodome (Gregory, 1933, p. 435). In Osteoglossidae the parasphenoid by means of basipterygoid processes constitutes an articulation with the pterygoidea and it furnishes the place for the attachment of teeth in this and other groups of Pisces (Gregory, 1933, pp. 164, 166).

b. The size

In Pisces, in which the parasphenoid fulfils this function of axis of the skull just mentioned, the parasphenoid is absolutely and especially relatively large and broad and firmly built. It extends far rostralwards to the ethmo-vomerine block and it extends also very far caudalwards, in certain Pisces as far as below the most rostral vertebrae (Marinelli, 1936, p. 211; Holmgren & Stensiö, 1936, p. 444; Stadtmüller, 1936, p. 640).

Concerning Sparidae, which possess extremely strong teeth, GREGORY (1933, p. 438) draws the attention to the great massiveness and strength of the parasphenoid.

In Acanthuriformes (Teuthioidei), Zanclidae and Balistidae with their extremely long snout the parasphenoid, which in Balistidae has developed a great median keel on its preorbital part, coöperates with the elongated and well-stiffened mesethmoid to form the base of the upper jaw and to support the snout (GREGORY, 1933, pp. 283, 284).

c. The position

In Pisces the parasphenoid, which fulfils the axis function just discussed, extends very far rostralwards and very far caudalwards on the ventral side of the neurocranium. In *Lophius* the parasphenoid has established a broad contact with the frontalia in front of the orbitae which braces the enlarged interorbital bridge (GREGORY, 1933, p. 396).

d. Homology and non-homology

The differences in size and position of the parasphenoid are not due to non-homology.

72. THE INTERORBITAL BRIDGE IN ITS AXIS FUNCTION

a. Introduction

One of the functions of the interorbital bridge is to constitute a firm axis for the skull. This applies mainly to tropidobasic skulls, in which owing to the reduction in the orbital part of the skull, the connection between the preorbital and the postorbital parts has become very weak indeed, if this connection is not strengthened by the parasphenoid just discussed and by the interorbital bridge to be treated in this paragraph. The demand for firmness in the connection between the preorbital and the postorbital parts of the skull, results from two facts, *viz.* that the snout of the skull functions as a bow and secondly that the pressure exercised by the teeth in the preorbital part of the skull, must be transferred to the postorbital part of the skull, to which the muscles of the jaws are attached. The latter function has already been discussed when treating the suspensorial mechanism of the new upper jaw, and we observed that the pressure exercised in biting and masticating is transferred from the preorbital part of the new upper jaw along the dorsal median part of the skull backwards. So there remains the discussion of the axis function of the interorbital bridge in relation with the function of the snout as a bow in swimming Vertebrata with a tropidobasic skull.

In the case of Pisces it is stated as a function of the interorbital bridge that it must obviously be strong enough to resist the pressure of the water above and in front; it must brace the ethmo-vomerine block in front and transmit some of its thrusts to the endocranial vault behind (GREGORY, 1933, p. 435) (see my figs 19, 25, 27, 50, 64, 120 a.o.). The interorbital bridge forms a beautiful arch, the thrusts of which are transmitted through spreading postorbital pillars, which rest on the prootica, the sphenotica and the pterotica (GREGORY, 1933, p. 437). But the interorbital bridge in Pisces has other functions besides, *viz.* it must afford a channel for the olfactory nerves and it must help to suspend the eyes (GREGORY, 1933, p. 435).

b. The size

It may be expected that the interorbital bridge, which fulfills the above mentioned axis function in swimming Vertebrata with a tropidobasic skull, will have a strong construction. However, the literature consulted did not contain special data on this point. GREGORY (1933, p. 438) only mentions the great massiveness and strength of the interorbital bridge in Sparidae with their strong teeth (see my fig. 89). Data on this matter concerning swimming Reptilia with a tropidobasic skull are lacking.

c. The position

The interorbital bridge is situated in and on either side of the dorsomedial line of the skull between the orbitae.

d. Homology and non-homology

Possibly the interorbital bridge in different species may not be composed of exactly the same elements of the skull. In this case it would not be strictly homologous and differences in size and position might partly be due to this fact.

73. SKELETON OF THE LIPS

a. Introduction

In cases, in which a skeleton of the lips occurs as labialia in lower Vertebrates, it is not an important element in the architecture of the skull, so we shall not enter into it in detail.

b. The size

The size of the skeleton of the lips in an absolute as well as in a relative sense, is connected with the size of the lips and so with that of the mouth opening or mouth slit (see my figs 61, 62). Concerning this we may refer to the discussion of the size of upper and lower jaws.

Relatively very well developed is the skeleton of the lips in Marsipobranchii (see my fig. 173).

c. The position

The skeleton of the lips is situated in the lips, so in the border of the mouth opening or mouth slit, in other words rostrally of the edges of the jaws. With relation to these edges of the jaws, there are no considerable differences; morphologically, however, diversities may be observed.

d. Homology and non-homology

Differences in size and position may partly be explained by non-homology of these skeletons of the lips in different systematic groups. At least numerous problems and opinions have been brought forward concerning the homologies of these and similar cartilages in Marsipobranchii, Selachii, Teleostei and larvae of Salientia (Stadtmüller, 1936, pp. 564/565).

74. SKELETAL ENVIRONMENT OF THE SPIRACULUM

a. Introduction

In some Teleostomi a very small paired spiraculum occurs, the skeletal environment of which has no appreciable influence on the architecture of the skull.

Holmgren & Stensiö (1936) mention a spiracular canal ("Spirakularkanal") in † *Birgeria* (p. 408), in Lepisosteidae (p. 471) and in † Perleididae, † Belonorhynchidae († Saurichthyidae) and Amiidae (pp. 418, 422, 449, 466, 469). In the last mentioned groups, however, they also call it a "Spritzlochkanal" (p. 455) or a "Spirakularöffnung" (p. 425).

b. The size

The paired spiraculum is always very small, in an absolute as well as in a relative sense.

c. The position

In † *Birgeria* the spiracular canal ("Spirakularkanal") pierces the cartilaginous wall caudally of the processus postorbitalis and also behind the sphenoid (Holmgren & Stensiö, 1936, p. 408).

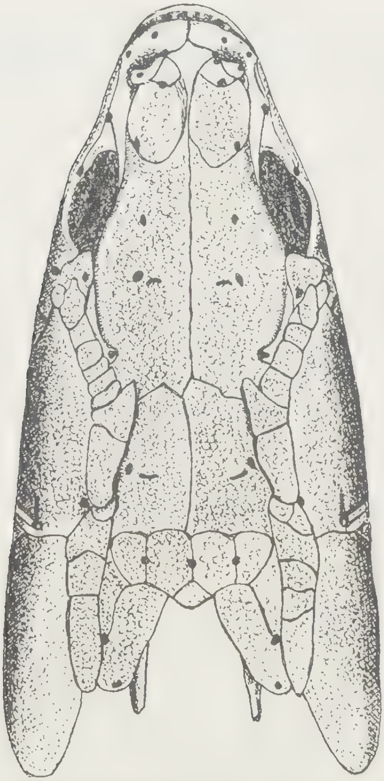

Fig. 172. *Polypterus bichir* Geoffr. Skull seen from the dorsal side. 1.5×. After Allis (1922), Pl. V, fig. 6.

In Lepisosteidae the spiracular canal ("Spirakularkanal") is situated near the postfrontal edge ("Postfrontalleiste") and the autosphenoticum (HOLMGREN & STENSIÖ, 1936, p. 471). HOLMGREN & STENSIÖ do not indicate the position of the spiracular canal ("Spirakularkanal") in † Perleididae, † Belonorhynchidae († Saurichthyidae) and Amiidae. However these authors do mention that it is situated near a supraspiracular ossicle ("Supraspirakularknochen") in † Perleididae (p. 420). Spiracular ossicles ("Spirakularknochen") – sometimes even several ossicles – occur in *Polypterus* (see my fig. 172) and besides in † Perleididae, also in † Palaeoniscidae and other Chondrostei (HOLMGREN & STENSIÖ, 1936, p. 397).

d. Homology and non-homology

The literature consulted does not indicate whether this opening might perhaps not be completely homologous in different systematic groups, which might afford an explanation for the differences in position.

75. BRANCHIAL SKELETON

a. Introduction

By branchial skeleton will be understood the continuous skeletal mass, which covers the branchial chamber in † Ostracodermi, the branchial basket in Marsipobranchii (see my fig. 173) and the branchial arches with a part of the hyoid arch in higher Pisces (see my figs 61, 62, 74, 114, 143 *c*, 174) and the larvae of Amphibia. The principal function of this branchial skeleton is to support the gills and the branchial region and to afford places of attachment for the respiratory muscles; in addition it has accessory functions with the ingestion and the conveyance of food.

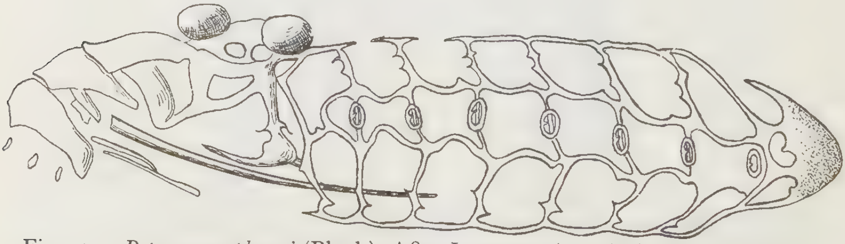

Fig. 173. *Petromyzon planeri* (Bloch). After LAMEERE (1947), fig. 245 on p. 251.

In the following discussion of the size and the position of the branchial skeleton, we shall leave out the radii branchiostegi, because their position and the space they occupy in the complex of the branchial skeleton are seldom exactly indicated. The number of the radii branchiostegi varies in Pisces (GREGORY, 1933, p. 427) (see my figs 42, 61, 62, 114, 143 *c*, a.o.).

In the following discussion of the size and the position the circumstance, whether the branchial arches are curved or not, will prove to be very important. In primitive Chordata, which were comparatively sluggish, bottom-living forms, the branchial arches were short and straight. Progressive selection for free-swimming led to the enlargement of the branchial arches, which would tend to bend and fold the enlarging branchial arches and to break them up into joints. Furthermore the advantages of a narrower head would have entailed obliquity of the branchial arches and their flexures in the lateral view. So the flexure of the branchial arches and the segmentation of these arches is secondary (GREGORY, 1933, p. 83). This flexure of the branchial arches occurs in two distinctly different forms. The Teleostomi possess V-shaped arches, in which the pharyngobranchialia project anteromesially and in which the ventral apices of the visceral arches are also pointed forward, seen from below. In Selachii the branchial arches are S-shaped, in this sense, that the top of the pharyngobranchialia adds a posteromesial projection to the dorsal leg of the lying V (GREGORY, 1933, pp. 81, 412). The segmentation of the hyoid arch allows of changes in the angle between hyomandibulare and hyoid, which has its influence on the shape of the hyobranchial skeleton and on the relative position of hyomandibulare and hyoid (LUTHER, 1938, p. 521).

b. The size

Exact data on the absolute and the relative size of the branchial skeleton are lacking.

The absolute size

The absolute size is, to a considerable degree, dependent on the absolute size of the body, of the head and of the skull. For in general there is a certain parallelism between these two measures. This parallelism, however, is interfered with by several other factors, which we shall discuss together with the relative size;

they are connected with the systematic group, with the number of branchial arches *etc*.

The relative size

In stages of development

Young larvae of "*Petromyzon*", contrary to the adult specimens, have a rather short branchial region (Holmgren & Stensiö, 1936, p. 295).

In adult animals

Concerning the extent in a rostro-caudal direction, we may first of all point out that on the one hand the † Ostracodermi, the Marsipobranchii and the Selachii possess a branchial skeleton which extends relatively very far caudalwards and which consequently is relatively very long, while on the other hand the † Arthrodira, Holocephali, Teleostomi and also the larvae of the Salientia have a much more tightly packed and shorter hyobranchial skeleton (Holmgren & Stensiö, 1936, pp. 334, 342) (see my figs 61, 62, 74). But also within these large groups all kinds of differences occur. Gregory (1933, p. 347) *e.g.* emphatically states that the branchial chamber in *Periophthalmus* is small.

In addition to these differences in the length of the branchial skeleton, which are characteristic of the large systematic groups, other divergences occur, which are connected with the number of branchial arches. This number is partly independent of the systematic position. Primarily the length of the branchial skeleton as a whole will show a certain parallelism to the number of branchial arches. In primitive cephalaspid † Ostracodermi there were nine visceral arches or interbranchial septa. In the existing Elasmobranchii the normal number of gills is five; the Hexanchidae possess six or seven gill-slits and *Pliotrema* six. In all ganoids and primitive Teleostei there are five gills, but in many of the more specialized Teleostei the number sinks to four and a half, four, three and one-half. In *Lycodontis* and in Gastrostomidae there has been a reduction in the size of the gill-arches (Gregory, 1933, p. 424). The number of gills and gill-slits quoted above after Gregory is of course connected with the number of branchial arches and their development.

c. The position

The position of the branchial skeleton is primarily determined by its connection with the neurocranium. In higher Pisces the branchial apparatus as a whole is connected with the neurocranium through the intervention of the small rod-like interhyale, which fits in a socket furnished by the symplecticum and the praeoperculum (GREGORY, 1933, pp. 438/439). But as the extent of the branchial skeleton in a caudal direction is rather indefinite, this suspension from the neurocranium by the interhyale does not give much information about the position of the branchial apparatus in relation to the neurocranium. For the extent of the branchial skeleton in the caudal direction is independent of the caudal limit of the dermatocranium and of the varying caudal limit of the primordial neurocranium (MARINELLI, 1936, pp. 211, 211 212).

The very considerable relative length of the branchial skeleton in † Ostracodermi, Marsipobranchii and Selachii is evident in the relatively far caudalward position of the hind limit of the branchial skeleton. However, there are differences in position, also between these three groups. In Marsipobranchii, in comparison with the cephalaspid † Ostracodermi, that part of the branchial arches that lies behind the so-called tongue, has been displaced backward (GREGORY, 1933, p. 99) (see my fig. 173). Also in Selachii the branchial skeleton extends very far caudalwards in the trunk and it is for a very considerable part situated just below the vertebral column; yet it extends relatively less far caudalwards than in Marsipobranchii (see my figs 61, 62). In Holocephali and Teleostomi the branchial skeleton is situated nearly entirely below the neurocranium, *viz.* below the parasphenoid (MARINELLI, 1936, p. 228) (see my figs 74, 114, 143 *c*). The fact that the skull of the Elasmobranchii is usually flatter (and, for that matter, also wider) than the skull of the Teleostei (GREGORY, 1933, p. 101), is perhaps partly due to this difference in the position of the caudal limit of the branchial apparatus and of the branchial apparatus as a whole.

We may point out in this place that according to GREGORY (1933, p. 269, fig. 145 A) the presence of an accessory respiratory organ in *Ophicephalus* may be responsible for the great increase in longitudinal diameter from the back of the orbita to the posterior rim of the enlarged suboperculum.

In the larvae of the Salientia the hyoid arch is suspended from the palatoquadratum (Stadtmüller, 1936, pp. 680, 684), which is one factor determining the position of the hyoid arch and also the position of the rostral limit of the branchial apparatus.

d. Homology and non-homology

In considering the size and the position of the branchial skeleton, we must bear in mind that there are considerable differences in the homology of the branchial skeleton in the various systematic groups.

The visceral skeleton in † Ostracodermi, that of the Marsipobranchii and that of the higher Pisces are three morphologically different formations. In † Ostracodermi the visceral skeleton is one continuous and undivided skeletal mass, which is very different from and quite differently constituted from the branchial basket of the Marsipobranchii (Holmgren & Stensiö, 1936, p. 271). And the branchial basket of the Marsipobranchii – whether taken with or without the skeleton of the mouth – is not easily comparable to the hyobranchial skeleton of the Selachii, Teleostomi, *etc.* and not completely homologous with it (Marinelli, 1936, p. 221; Holmgren & Stensiö, 1936, pp. 238, 295/296).

But also within the groups of the Selachii and the Teleostomi differences in size and position occur, which are due to differences in the number of branchial arches and so the question arises whether the whole branchial skeleton of one group is completely homologous with that of another group or not.

76. PHARYNGEAL BONES

a. Introduction

The ossa pharyngea which are present in a number of Teleostei are not very important in relation to the architecture of the skull, so we shall discuss them only superficially, which is the more justified because parts of the dentigerous plate, situated on the pharyngeal bones, have already been considered.

We shall take the data from Gregory (1933), though this author speaks of upper and lower pharyngeal "bones" only in the case of *Fundulus similis* (Brd. & Gir.) and *Opsanus tau* (L.) (pp. 219, 383). Everywhere else he mentions upper and lower pharyngealia, by which is understood dentigerous plates on pharyngobranchialia and on ceratobranchialia (p. 90).

b. The size

The ossa pharyngea may be called small in an absolute as well as in a relative sense.

c. The position

The upper pharyngeal bone or upper pharyngeale is a dentigerous plate on the fourth pharyngobranchiale and the lower pharyngeal bone or lower pharyngeale is a dentigerous plate on the fifth ceratobranchiale (GREGORY, 1933, pp. 90, 423/424, see also p. 193). But in the case of *Fundulus similis* (Brd. & Gir.) GREGORY (1933, p. 219) also speaks of the three superior pharyngealia on each side.

Moreover the lower pharyngeal bones or lower pharyngealia may be situated medially or to the right and left of the median line, which becomes apparent from their contact or connection in the median plane, *e.g.* in Synentognathi, in which they are coalesced or fused (pp. 221, 223), further by their fusion in Labridae (p. 256) and Scaridae (p. 258), by the suture in *Fundulus* (p. 219), in some of the Cyprinodontes (p. 223) and in Cichlidae (pp. 254/255); further they are united in *Pogonias* (p. 252) and in Pomacentridae (p. 255).

d. Homology and non-homology

In those cases in which the upper pharyngeal bone is fused with one specific pharyngobranchiale, these pharyngeal bones are homologous in all species, at least when the same consecutive number expresses homology of the branchial arches in question. In *Fundulus similis* (Brd. & Gir.), in which three superior pharyngealia occur instead of one on the fourth pharyngobranchiale, these three are not mutually homologous.

When the lower pharyngeal bone is fused with one specific ceratobranchiale, these pharyngeal bones are homologous in all species, at least when the same consecutive number expresses homology of the branchial arches in question.

77. SUSPENSORIAL MECHANISM OF THE PECTORAL GIRDLE

a. The size

In † Ostracodermi, in which the endoskeleton of the pectoral girdle is continuous with the neural endocranium and with the visceral endoskeleton, the suspensorial mechanism may certainly be called broad and large (Holmgren & Stensiö, 1936, pp. 233, 251, 260, 270).

In Selachii the most caudal branchial arch is built very stoutly in connection with the attachment of the pectoral girdle to the branchial skeleton; in Teleostomi, in which this function is not fulfilled by the most caudal branchial arch, this arch is not strongly developed.

In Batoidei the separate antorbital cartilage ("Schädelflossenknorpel"), which supports the strongly developed pectoral fin, may be very large (Holmgren & Stensiö, 1936, p. 310).

The paired, lateral process of the ethmoidal region, which in † Stegoselachii fulfills the same function, is large (Holmgren & Stensiö, 1936, p. 326).

In Teleostei the pectoral girdle may be suspended from the caudal surface of the temporal region. In this case it is one of the functions of the endocranial vault or brain case proper to afford a support and anchorage for the shoulder girdle (Gregory, 1933, p. 435).

b. The position

In † Ostracodermi the continuous connection is so broad that it cannot be called a definite place of attachment.

In Selachii the suspensorial mechanism is situated at the caudal end of the branchial apparatus.

In Batoidei the antorbital cartilage ("Schädelflossenknorpel") is attached to the ethmoidal region. The same applies to the suspensorial mechanism in † Stegoselachii.

In Teleostomi the suspensorial mechanism is attached to the temporal region of the neurocranium (see my figs 18, 19, 114, 143 *c*, a.o.).

c. Homology and non-homology

In considering the size and position of the suspensorial mechanism of the pectoral girdle, we must bear in mind that this mechanism in † Ostracodermi, in Selachii, in Batoidei and in Teleostomi belongs to four morphologically different formations. The broad continuous connection in † Ostracodermi is not homologous with the most caudal branchial arch in Selachii and not with the suspensorial mechanism in the ethmoidal region in Batoidei and † Stegoselachii or with that in the temporal region in Teleostomi.

The antorbital cartilage ("Schädelflossenknorpel") of the Batoidei is sometimes considered to be homologous with the processus ectethmoidalis ("Ectethmoidfortsatz") of the Squaliformes (HOLMGREN & STENSIÖ, 1936, p. 310).

78. PERICARDIAL CAPSULE AND CARDIOBRANCHIALE

a. The size

The pericardial cartilage of the Marsipobranchii is small in an absolute sense, but rather large in a relative sense.

The same may be said of the cardiobranchiale of the Selachii.

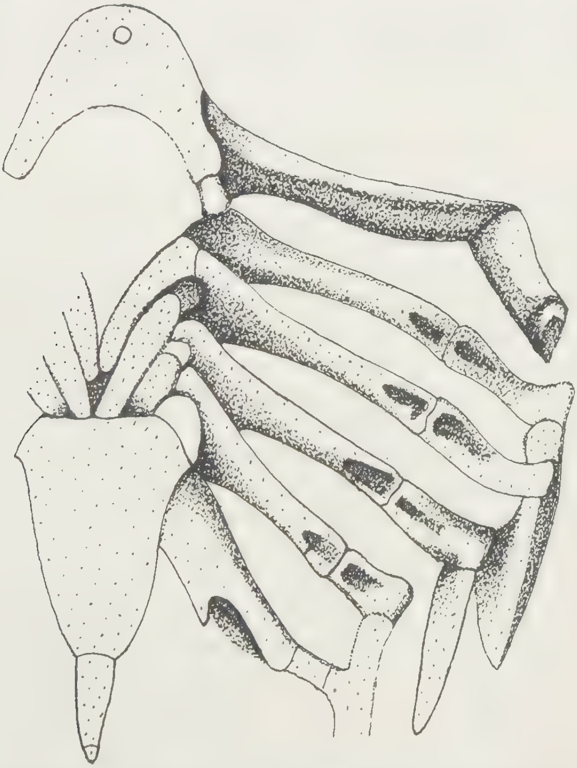

Fig. 174. *Scylliorhinus stellaris* (L.) (*Scyllium catulus*). Right half of the branchial skeleton, seen from the dorsal side. 1.5×. After GEGENBAUR (1872), Table XVIII, fig. 4.

b. The position

The pericardial cartilage of the Marsipobranchii constitutes the most caudal part of the ventral part of the branchial basket (see my fig. 173).

The cardiobranchiale is the most caudal copula of the branchial skeleton in Selachii (see my fig. 174).

c. Homology and non-homology

As the branchial basket of the Marsipobranchii and the hyobranchial skeleton of the Selachii are not or at least not completely homologous and as moreover their caudal limits are not identical, the pericardial cartilage of the Marsipobranchii and the cardiobranchiale of the Selachii are not homologous. This is also apparent from the different position with regard to the heart, *viz.* caudally in Marsipobranchii and dorsally in Selachii.

79. OPERCULUM

a. Introduction

By operculum we shall understand the series of bony plates, which in the higher Pisces cover the gill chamber laterally; it is composed of the praeoperculum and the opercular series (operculum, suboperculum and interoperculum) (see my figs 114, 143 *c*, a.o.).

As the operculum is always situated between the suspensorium of the jaw and the pectoral girdle, its size and position are strictly defined (see my figs 114, 115, 116, 143 *c*, a.o.).

The praeoperculum, which is usually a crescentic or boomerang-like bone, follows the general curve of the suspensorium, covers the hyomandibulare laterally and fits between a vertical crest of the hyomandibulare and the anterior border of the opercular fold (GREGORY, 1933, pp. 90, 426). According to GREGORY (1933, p. 427) the position of the suspensorium is one of the leading factors in the position of the praeoperculum and the preopercular fold seems to have essentially the same relation to the quadratum and metapterygoid that the opercular fold (including the operculum itself, the inter- and suboperculum) has to the segments of the hyoid arch. The hyomandibulare bears posterolaterally the operculum and the suboperculum, while the interhyale is covered laterally by the interoperculum (GREGORY, 1933, p. 90). In Teleostei – with only very few exceptions – the operculum is attached by a concave facet to the opercular pedicle of the hyomandibulare (pp. 425, 426). This fact also points to a connection between size, form and position of the opercular series and the shape and position of the hyomandibulare.

The caudal border of operculum and suboperculum – so of the whole opercular series – is always adjusted to the curve of the cleithrum (GREGORY, 1933, p. 426).

Secondly the size and consequently also the position of the praeoperculum and opercular series are determined by the size and modifications of the gill apparatus, that are connected with different types of respiration (GREGORY, 1933, p. 84).

Finally the position and consequently the shape of praeoperculum and opercular series are also determined by the shape of the streamlined head and skull (VAN DER KLAAUW, 1945, p. 36). As GREGORY (1933, p. 84) expresses it: there is a close connection with the head form and body form.

b. The size

Exact data on the size of the operculum are lacking.

The absolute size

Generally speaking there is a parallelism between the size of the operculum and the size of the skull, in this sense that absolutely large opercula are found in absolutely large skulls and small opercula in absolutely small skulls.

This parallelism, however, is interfered with by other factors, which will be discussed in connection with the relative size. We only mention the different degree of development of the gill apparatus in animals of the same size, but of different species with divergent respiratory capacity.

In large Pisces the operculum may be called very large and in small Pisces it may generally be called at least large.

The relative size

In stages of development

Though data on the relative size of the operculum in stages of development in Pisces are unknown to me, we must for a moment dwell upon the shape of the rostral border of the operculum and its distance from the orbita, because these two factors are important in determining the size of the operculum and moreover they offer an explanation of the conditions in adult Pisces.

In the embryonic and larval stages of many Teleostei the praeoperculum is pressed close to the eye and the entire opercular fold is brought into close proximity with the eye and consequently the praeoperculum and the opercular series show a lunate and circumorbital arrangement (Gregory, 1933, pp. 426, 427, 428, 439, 450). In part of the Teleostei this close proximity to the eye persists in later ontogenetic stages up to the adult stage. In many species of Teleostei, however, as development proceeds the opercular fold is displaced backward and the praeoperculum and the opercular series move backward from the eye, through which the space between the opercular flap and the orbita will increase (Gregory, 1933, pp. 428, 430, 450). Nevertheless praeoperculum and opercular series still retain more or less of their circumorbital arrangement (p. 450).

In adult animals

As reminiscence of the larval stages the circumorbital arrangement of the praeoperculum and of the opercular series persists in the adult stages of the oldest † Protospondyli; even after the lengthening of the space between the opercular flap and the eye, the opercular series retains a good deal of its "circumorbital" appearance and arrangement (Gregory, 1933, pp. 428, 450).

In many adult Teleostei, too, the position of praeoperculum and opercular series close behind the orbita has been retained (Gregory, 1933, pp. 426, 427, 428) (see my figs 27, 29). In many other species of adult Teleostei, however, the distance between the rostral border of the operculum and the caudal border of the orbita has increased, as we have seen above (see my figs 28, 30, 42, 64, 81, 85, 86, 88, 115, 120, 121, 125, 129, 146).

The circumorbital arrangement is the consequence of the connection with the suspensorium of the jaw, which is sometimes curved very far rostralwards. This shape influences the size of the operculum.

When the quadratum-articulare joint is shifted forward, as is the case in many small-mouthed Pisces, the lower end of the praeoperculum follows it; the upper end also follows the general line of the suspensorium (Gregory, 1933, p. 427) (see my figs

43, 66, 91, 93, 117, 118, 143 *d*). In the discussion of the position of the operculum we shall treat in detail two extreme instances of this situation, *viz. Fundulus* and *Fistularia* (GREGORY, 1933, pp. 217, 225) (see my figs 93 *a*, 143 *d*).

The opposite case also occurs, *viz.* a quadratum-articulare joint, which is situated far caudalwards and this also considerably influences the size of the operculum. For when the quadratum-articulare joint lies far caudalwards, the suspensorium is inclined from dorsorostral to ventrocaudal and the praeoperculum follows this slope of the hyomandibualre. This is to a high degree the case in † Palaeoniscidae and in † Belonorhynchidae († Saurichthyidae), less so in † Perleididae and still less so in † Ospiidae. One consequence a.o. is that the interoperculum is lacking in † Perleididae, while it is present still in † Ospiidae (HOLMGREN & STENSIÖ, 1936, pp. 398/399, 415, 420, 421, 426) (see my figs 76, 77, 95, 116, 143 *a*).

As to the influence of the caudal border on the size of the operculum, GREGORY (1933, p. 299, fig. 174) mentions that the very peculiar downward and backward turning of the cleithrum in *Lampris luna* (Gmel.) may have influenced the notable spreading of the praeoperculum and operculum in the same general direction.

However important the knowledge of the shape of the rostral border of the operculum and of the position of the rostral and caudal borders of the operculum (resp. of the suspensorium and of the pectoral girdle) may be, in the last instance it is the distance between these rostral and caudal borders, which is material in judging of the size of the operculum.

In this connection we may point to the following data given by GREGORY (1933). In *Mugil cephalus* L. there is a marked anteroposterior expansion of the operculum and a backward prolongation of the praeoperculum and interoperculum, in other words the operculum is long in a rostrocaudal direction (GREGORY, 1933, pp. 263/264, fig. 138). In *Scomber* and allied Scombroidei there is a marked anteroposterior elongation of their praeoperculum and operculum and consequently of the entire operculum; this is probably conditioned by the voluminous development of the branchial apparatus of these very fast swimming fishes (p. 309, fig. 188). In Xenopterygii there is a strange backward growth of the operculum and suboperculum and so of the operculum as a whole, which is possibly due to the presence of the great pelvic sucking disc, the muscles of which perhaps find their origin on the operculum (p. 372, fig. 249).

But to gain an insight into the relative size of the operculum not only the distance between rostral and caudal border of the operculum, but also its height must be known.

In a few cases GREGORY (1933) mentions besides the rostrocaudal length also the height of the operculum. *E.g.* in *Antennarius* and allied Pediculati the space between the hyomandibulare and the shoulder-girdle is very narrow in proportion to its height; the entire operculum is correspondingly narrow and high (p. 392, fig. 265). Also in *Lophius* an extension and marked narrowing of the opercular apparatus occurs (p. 394, fig. 267). In Ogcocephalidae (p. 401, fig. 269) (see my fig. 67) the elements of the opercular apparatus are secondarily enlarged in comparison with the situation in *Antennarius* and *Lophius*. Between *Antennarius* and *Lophius* on the one hand and the Ogcocephalidae on the other hand stands *Chaunax* (GREGORY, 1933, p. 401, fig. 271). In *Chaetodon* the opercular elements share in the general deepening of the skull, which is very high indeed, moreover the operculum is very narrow (GREGORY, 1933, p. 279, fig. 155). – Also in *Capros aper* (L.) the opercular region is much deepened vertically and shortened anteroposteriorly (GREGORY, 1933, p. 273, fig. 149 A).

Besides these data on the length and the height of the operculum, GREGORY (1933) also gives some data on the superficial area of the operculum as a whole.

The opercular region is enlarged in *Ophicephalus*, *Osphronemus* and other Pisces with enlarged respiratory chamber (GREGORY, 1933, p. 426, figs 145, 147).

A very small operculum is mentioned by GREGORY in the following cases. In *Lycodontis funebris* (Ranzani) the upper two-thirds of the opercular series has been sacrificed in order to make room for the swelling movements of the branchial syringe and the opercular apparatus has become almost vestigial (GREGORY, 1933, pp. 202, 426, fig. 82 B) (see my fig. 119). In Gonostomidae, such as *e.g. Gonostoma elongatum* Gthr, the opercular system has become extremely narrow and consequently decreased in superficial area (p. 426, fig. 53). In Gastrostomidae the opercular system has disappeared, probably in connection with the great distensibility of the mouth and throat (p. 426) (see my fig. 87). Also in *Periophthalmus* the branchial chamber is small and with it the opercular series (Gregory, 1933, p. 347, fig. 228) (see my fig. 41).

In an absolute sense it is hardly possible to speak of a definite size of the operculum in a particular specimen, because with the movements of the operculum the outline is changed by the muscles (Gregory, 1933, p. 426) and with it also the superficial area of the operculum.

c. The position

In stages of development

As we have already seen in the discussion of the size of the operculum, in the embryonic and larval stages of many Teleostei the preopercular region shows a close appression to the eye and the entire opercular fold is brought into close proximity to the eye, so as to form practically the posterior border of the eye (Gregory, 1933, pp. 426, 427, 428). To this position against the orbita in larval stages also points the lunate and circumorbital arrangement of the praeoperculum and the opercular series, which to a considerable extent is conditioned both by the large size of the eyes and by the smallness of the mouth (pp. 439, 450).

We have also seen above that in part of the Teleostei this close proximity to the eye persists in later ontogenetic stages, but that in many other species of the Teleostei as development proceeds the opercular fold is displaced backward and the praeoperculum and the opercular series move backward from the eye, by which the space between the opercular flap and the orbita will increase (Gregory, 1933, pp. 428, 430, 450). As the circumorbital arrangement is still more or less retained, the dorsorostral end reaches rather far and the ventrorostral end sometimes even very far rostralwards.

In adult animals

In the discussion of the size of the operculum in adult Teleostei we have seen that, however much the distance to the caudal border of the orbita may change, praeoperculum and opercular series retain a good deal of the "circumorbital" arrangement and appearance (Gregory, 1933, pp. 428, 450). This entails that the dorsorostral and ventrorostral end of the operculum project more or less rostralwards with regard to the general direction of the axis of the praeoperculum.

In some cases the rostroventral end is situated extremely far rostralwards, *viz.* when the quadratum-articulare joint is shifted forward, as in many small-mouthed fishes, the lower end of the praeoperculum follows it; the upper end also follows the general line of the suspensorium (GREGORY, 1933, p. 427). As examples GREGORY (1933) mentions *Fundulus* and *Fistularia*. In *Fundulus* the prae- and interoperculum are also involved in the forward growth of the suspensorium (p. 217, fig. 96 A). In *Fistularia*, in which the quadratum-articulare joint is shifted extremely far rostralwards, the elongated interoperculum and praeoperculum lie beneath the long tube, which extends between lower jaw and eye (GREGORY, 1933, p. 225, fig. 105) (see my figs 93 *a*, 143 *d*).

When the longitudinal axis of the praeoperculum is inclined from dorsorostral to ventrocaudal, the rostroventral end of the praeoperculum, though it curves rostralwards, naturally does not reach a very forward position.

Moreover the rostral border of the operculum may be situated at only a little distance from the caudal border of the orbita – just as in the ontogenetic stages – but a lengthening of the space between the operculum and the orbita may also occur (GREGORY, 1933, pp. 426, 427, 428).

The position in a rostrocaudal sense is also influenced by the direction of the longitudinal axis of the praeoperculum. This direction may be approximately vertical (see, my figs 90, 126, 129, 143 *b*), it may slope from dorsocaudal to ventrorostral and it may also be inclined from dorsorostral to ventrocaudal. As this direction of the longitudinal axis of the praeoperculum shows a rather strict parallelism with the direction of the longitudinal axis of the suspensorium, we may with regard to examples refer to the discussion of the suspensorium.

As to the mutual position of left and right operculum in a lateral sense, we may point out that the distance between the opercula may be very divergent, dependant on the breadth of the head in this place.

GREGORY (1933, p. 427, figs 267, 272) points out that in Pediculati the opercular apparatus as a whole is naturally much influenced by the great expansion of the pharynx and this applies undoubtedly to the mutual position of left and right opercular series.

Considering all data concerning the position of the opercula, especially on the position in a transverse sense, we must always bear in mind that this position is changed to a considerable extent by the contractions of the muscles.

d. Homology and non-homology

Differences in size and position of the operculum cannot be explained by non-homology, for the operculum is homologous in all Pisces, in which it is present.

80. HYOID SKELETON

a. Introduction

The size and position of the hyoid skeleton in Tetrapoda, is closely related with the functions it fulfils. Some functions of the hyoid skeleton are a.o.: to furnish places of attachment for the muscles of the tongue (see my fig. 158), to play a part in the movements of the tongue in connection with the ingestion of food, expansion of the mouth cavity in respiration and sound production [1]).

b. The size

The size of the hyoid skeleton depends on a number of factors, a.o. on the number of arches, on the extent to which the arches are ossified or ligamentous and on the length of the arches.

The absolute size

This size of the hyoid skeleton of the Tetrapoda may be very divergent.

Generally speaking there is a certain parallelism with the body size of the animal. But this parallelism is interfered with by several other factors. One of these is the different number of arches in the different classes, *viz.* in Reptilia and Aves the number of arches is greater than in most Mammalia, however in Monotremata among the Mammalia a greater number of arches is found as in Sauropsida. Secondly there is a connection with the protrusibility of the tongue in those groups, in which the movements of the tongue depend almost entirely on the movements of the hyoid skeleton as in Caudata and in Aves. As examples we mention the Trochilidae, Picidae and *Hydromantes* (*Spelerpes*), in which the cornu branchiale I is exceedingly long (STADTMÜLLER, 1936, p. 687; MARINELLI, 1936, p. 835). Moreover there is a connection between the length of the hyoid arch and the size of the pieces of food to be ingested in those cases in which the hyoid arch is entirely skeletal (STRESEMANN, 1934, p. 804). In cases, in which, as in *Homo*, the hyoid arch is ligamentous for a considerable part of its length, the hyoid skeleton is consequently smaller than in species of the same body size, but with an entirely skeletal cornu hyale.

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[1]) On size, shape, function *etc.* of the hyoid apparatus, see: J. M. SPRAGUE (1941). A study of the hyoid apparatus of the Cricetinae. J. Mammal., **22**, pp. 296—310. – J. M. SPRAGUE (1942). The hyoid apparatus of Neotoma. J. Mammal., **23**, pp. 405—411. – J. M. SPRAGUE (1943). The hyoid region of placental mammals with especial reference to the bats. Amer. J. Anat., **72**, pp. 385—472. – J. M. SPRAGUE (1944). The hyoid region in the Insectivora. Amer. J. Anat., **74**, pp. 175—216. (Postwar addition in the manuscript)

The relative size

Because of the greater number of cornua, the relative size of the hyoid skeleton in Sauropsida and in Monotremata is primarily greater than in higher Mammalia. Nevertheless the hyoid skeleton is also in higher Mammalia a relatively large element of the skull. In Salientia the hyoid skeleton may be called very large.

The connection with the protrusibility of the tongue in Aves is clearly demonstrated by the relatively very considerable length of the hyoid skeleton in Picidae. In *Dryobates major* (L.) the hyoid skeleton is $2^1/_2$ times as long as the upper bill, in *Dryocopus martius* (L.) three times, in *Picus viridis* L. four times and in *Jynx torquilla* L. five times (STRESEMANN, 1929, pp. 457/458; BÖKER, 1937, p. 91). In Trochilidae the cornua hyalia are definitely shorter than in Picidae (BÖKER, 1937, p. 99).

In Primates the corpus hyoidei is a broad somewhat concave shield; in some genera this concavity is rather deep; in *Alouatta* (*Mycetes*) it constitutes the osseous bulla hyoidea (GÖPPERT, 1937, pp. 839, 860, 862).

c. The position

In the discussion of the position of the hyoid skeleton it is necessary to consider the position with respect to the skeleton of the larynx and with respect to the skull proper, the attachment to the skull as well as its general position with regard to the skull.

The skeleton of the larynx in Salientia shows connections with the hyoid skeleton, because of the function which the hyoid skeleton fulfils in the respiratory movements and the production of sound (STADTMÜLLER, 1936, p. 658).

As to the attachment of the hyoid skeleton to the skull, we may consider as the normal condition, that the hyoid arch is suspended from the otic capsule.

In Picidae with their exceedingly long cornua hyalia the proximal ends of the cornua hyalia are attached to the root of the upper bill; they even penetrate into the upper bill itself, sometimes as far as in the tip of the praemaxillare, which means as far rostrally as possible. From here to the distal end of the cornu hyale – so near the corpus hyale – the long cornu hyale passes along the entire cerebral skull and along the neck. In cases in which the cornu hyale is exceedingly long, it hangs in a loop far into the region of the neck, as in *Picus viridis* L. and in *Jynx torquilla* L. (BÖKER, 1937, pp. 91/92). In *Dryobates villosus* (L.) the cornua hyalia have grown in three quarters of a circle round the right eye (BÖKER, 1937, p. 92). In Trochilidae, in which the cornua hyalia are definitely shorter than in Picidae, the cornua extend only to the upper ridge of the bill ("Schnabelfirst") (BÖKER, 1937, p. 99).

The position of the hyoid skeleton may be more or less divergent. In Salientia, at least after metamorphosis, and in Mammalia the hyoid skeleton is little mobile. But in Caudata and in Aves, in which the tongue in its movements is nearly entirely dependent on the movements of the hyoid skeleton, the position of the hyoid skeleton with regard to the rest of the skull, may be changed considerably (STADTMÜLLER, 1936, pp. 658, 680/681, 685).

d. Homology and non-homology

Considering the size and the position of the hyoid skeleton of the Tetrapoda, we must bear in mind that, though the cornu hyale is comparable only to the ventral half of the hyoid arch of the Pisces, it nevertheless generally extends as far as the otic capsule. Moreover we must remember that in the hyoid skeleton of the higher Mammalia the cornua branchialia 2 and 3 are lacking; they have separated from the hyoid skeleton and joined the skeleton of the larynx as cartilago thyreoides.

81. SKELETON OF THE LARYNX

a. The size

The absolute size

There is a certain parallelism between the size of the skeleton of the larynx and the body size of the animal, in this sense, that absolutely large animals have an absolutely large skeleton of the larynx and absolutely small animals an absolutely small skeleton of the larynx. But this parallelism is interfered with by other factors. *E.g.* there is an interference by the number of components in the different higher systematic groups, in this sense, that in higher Mammalia the cornua branchialia 2 and 3 also are part of the skeleton of the larynx as the so-called cartilago thyreoides. Therefore the skeleton of the larynx in higher Mammalia is primarily larger in an absolute sense. Moreover the parallelism with the body size may be interfered with in the case of functions in sound producing, sucking, sometimes also in connection with the sex. These cases will be treated in more detail in the discussion of the relative size.

The relative size

In higher Mammalia the skeleton of the larynx is relatively large in comparison to that of the Non-Mammalia and Monotremata, at least primarily, because of the reason mentioned above. In a relative sense the skeleton of the larynx in higher Mammalia may be called fairly large.

In the bat *Epomophorus monstrosus* (Allen) (*Hypsignathus monstrosus*) the larynx is relatively very large, because this animal sucks out figs (Böker, 1937, p. 111).

Among Mammalia sometimes definite differences in the size of the larynx are apparent between the two sexes (Weber, 1927 I, p. 410).

b. The position

The skeleton of the larynx is situated caudally of the hyoid skeleton, but apart from this, considerable differences occur with regard to the position in a dorsoventral as well as in a rostrocaudal direction.

In lower Vertebrata the entrance to the larynx is situated on the bottom of the mouth-pharynx cavity; while in Mammalia the larynx lies far dorsally and extends upwards as far as the caudal border of the soft velum palatinum ("Gaumensegel") (Böker, 1937, p. 136). In some Mammalia, *e.g.* in Cetacea, *Talpa* and in many Rhinolophidae, the entrance to the larynx is kept fixed in position in the cavum pharyngo-nasale (Böker, 1937, pp. 136/137). In *Epomophorus monstrosus* (Allen) (*Hypsignathus monstrosus*) the exceedingly large larynx extends caudalwards along the region of the neck and through the thorax as far as the diaphragma (Böker, 1937, p. 111).

As to the position in a rostrocaudal sense we observe that normally the larynx is situated in the region of the neck and extends at farthest to the most caudal part of the cavum pharyngo-nasale. In Serpentes, however, the larynx is situated very far rostralwards in the proximity of the symphysis of the lower jaw (Böker, 1937, p. 136).

The position of the skeleton of the larynx is not fixed. For in several groups the larynx can be drawn up, *e.g.* in many Mammalia; in other Mammalia on the contrary the entrance to the larynx is fixed, as we have already mentioned in the case of the Cetacea, *Talpa* and many Rhinolophidae (Böker, 1937, pp. 136/137). In Aves the larynx may also be able to change its place (Göppert, 1937, p. 825).

c. Homology and non-homology

In considering the differences in size and position of the skeleton of the larynx, we must bear in mind that this skeleton in higher Mammalia is not completely homologous with that of the lower Vertebrata, because in higher Mammalia the cornua branchialia 2 and 3 have been joined to the skeleton of the larynx.

82. CARTILAGO EPIGLOTTICA

a. The size

The cartilago epiglottica may be called small in an absolute as well as in a relative sense.

b. The position

The position of the cartilago epiglottica is determined by het position of the rostral end of the trachea, the entrance to which can be closed by it.

83. TRACHEA

a. The size

In a number of cases the length of the trachea and bronchi may change when the neck is stretched, either because the bronchi, which are lying in loops are partly straightened out, as may occur in Testudinides (Göppert, 1937, p. 819), or by lengthening of the trachea itself, as may occur in Testudinides

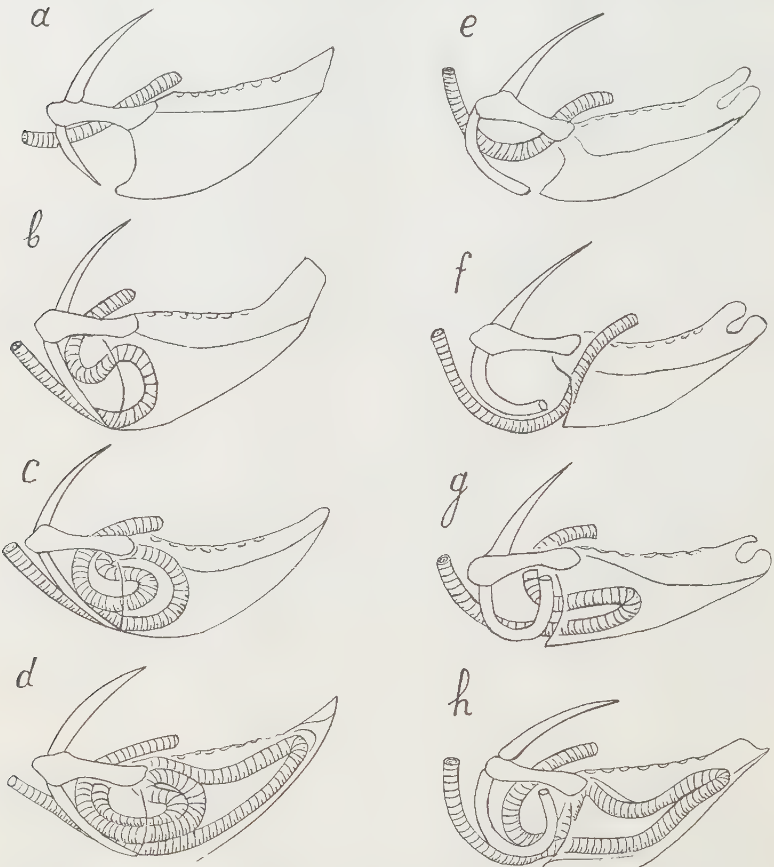

Fig. 175. Diagrams of the sternal handles of the trachea in the evolutionary lines of the Grues (*a–d*) and of the Cygninae (*e–f*). *a. Psophia crepitans* L. *b. Anthropoides virgo* (L.). *c. Grus antigone* (L.). *d. Grus americana* (L.). *e. Cygnus melancoriphus* (Molina). *f. Chenopsis atrata* (Lath.). *g. Cygnus cygnus* (L.). *h. Cygnus buccinator* Richardson. After Portmann (1950), fig. 207 on p. 264.

and in Aves (GÖPPERT, 1937, p. 819; STRESEMANN, 1937, p. 872) (see my fig. 175).

A curved neck in a bird is not always accompanied by a curved trachea (STRESEMANN, 1937, p. 880).

As we mentioned above the trachea may be curved in the region of the neck as well as intrathoracally as in Testudinides and in Aves, in some cases in both sexes, sometimes in the males only (GÖPPERT, 1937, p. 830; STRESEMANN, 1937, pp. 872/873) (see my fig. 175). In Mammalia a curved trachea may also occur, *e.g.* in *Bradypus* (GÖPPERT, 1937, p. 863).

Local dilatations of the trachea and the bronchi are known in Aves, especially in the form of a syrinx, sometimes differently developed in the two sexes (STRESEMANN, 1937, pp. 873–876, 881). But also in a few Mammalia local dilatations are found (GÖPPERT, 1937, p. 863).

Taking into account these peculiarities and their influence on the length and width of the trachea and bronchi, we may make the following observations.

The absolute size

The absolute size of the trachea depends on the absolute body size of the animal, on the length of the neck and on the fact, whether the trachea is coiled or not. Very large, in an absolute sense is the trachea in very large species, as in *Elephas* and *Struthio* and in species with a very long neck as in *Giraffa* and *Ardea*. The trachea is absolutely small in very small species, such as Salientia, small Aves, small Mammalia *etc.* and in species with a very short neck, as Salientia. A short trachea is found in Cetacea and Sirenia (GÖPPERT, 1937, p. 863).

The relative size

In a relative sense the trachea is always large, sometimes even very large, especially when the neck is very long and the trachea is coiled.

b. The position

The trachea is situated in the region of the throat, the neck and the rostral part of the thorax.

84. PADDING ELEMENTS

a. Introduction

Between different functional components of the skull padding elements occur. These may be formed by solid bone, spongy bone and pneumatic bone. If we define the cerebral capsule as the thin plate or layer of bone lining the cavity for the brain in the skull, and the place of attachment of a certain neck muscle the rather thin plate or layer of bone on the surface of the skull to which this neck muscle is attached, the space between these two functional components of the skull is sometimes filled by padding elements as mentioned. This condition may be found in many places of the skull in a number of Vertebrata.

A more critical approach to this question, however, will show that the spongy *etc.* bone mentioned above as an example, does not act as a padding element only, but belongs functionally to the cerebral capsule as well in sofar as it bears and protects it and also to the place of attachment of the neck muscle in so far as it shows the influence of the attachment of the muscle on the structure of the bone in the presence of trabeculae beneath the most superficial layer of compact bone. Our knowledge, however, is too scanty to distinguish in the padding element mentioned the part belonging to the functional components mentioned and the padding element as such.

b. The size

The size of the padding elements is very divergent in different Vertebrata, even in nearly related groups and even in specimens of different age (see my figs 1, 2, 4). The literature consulted gives no exact data.

In most Aves the padding elements are absent or practically absent. In some Aves, however, as *e.g.* in *Buceros* (see my fig. 15), it is well developed.

In some marine Vertebrata the padding elements are strongly developed and made up of solid bone.

c. The position

The literature consulted gives no exact data on the position of the padding elements of the skull, which are no doubt a very important element for its architecture.

LITERATURE CITED

ARIENS KAPPERS, C. U., 1934: Feinerer Bau und Bahnverbindungen des Zentralnervensystems. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd II, 1. Hälfte, 319-486. – Berlin & Wien, Urban & Schwarzenberg.

BALLOWITZ, E., 1938: Elektrische Organe. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd V, 657-682. – Berlin & Wien, Urban & Schwarzenberg.

BOAS, J. E. V., 1934: Äusseres Ohr. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd II, 2. Hälfte, 1433-1444. – Berlin & Wien, Urban & Schwarzenberg.

BÖKER, H., 1935: Einführung in die vergleichende biologische Anatomie der Wirbeltiere, Bd I. – Jena, G. Fischer, XII + 228 pp.

———, 1937: Einführung in die vergleichende biologische Anatomie der Wirbeltiere, Bd II: Biologische Anatomie der Ernährung. – Jena, G. Fischer, XII + 258 pp.

BURLET, H. M. DE, 1934: Vergleichende Anatomie des stato-akustischen Organs. a) Die innere Ohrsphäre. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd II, 2. Hälfte, 1293-1380. – Berlin & Wien, Urban & Schwarzenberg.

———, 1934: Vergleichende Anatomie des stato-akustischen Organs. b) Die mittlere Ohrsphäre. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd II, 2. Hälfte, 1381-1432. – Berlin & Wien, Urban & Schwarzenberg.

DUBOIS, E., 1897a: De verhouding van het gewicht der hersenen tot de grootte van het lichaam bij de zoogdieren. – Verh. Kon. Akad. Wetensch. Amsterdam, Tweede Sectie, **5**, Nr 10, 1-41.

———, 1897b: Sur le rapport du poids de l'encéphale avec la grandeur du corps chez les Mammifères. – Bull. Soc. d'Anthropologie de Paris, ser. 4, **8**, 337-376.

———, 1897c: Über die Abhängigkeit des Hirngewichtes von der Körpergrösse bei den Säugethieren. – Arch. Anthropologie, **25**, 1-28.

———, 1898: Über die Abhängigkeit des Hirngewichtes von der Körpergrösse beim Menschen. – Arch. Anthropologie, **25**, 423-441.

———, 1913: De betrekking tusschen hersenmassa en lichaamsgrootte bij de gewervelde dieren. – Versl. Kon. Akad. Wetensch. Amsterdam, **22**, 593-614.

———, 1914a: On the relation between the quantity of brain and the size of the body in Vertebrates. – Proc. Kon. Akad. Wetensch. Amsterdam, **16**, 647-668.

———, 1914b: Die gesetzmässige Beziehung von Gehirnmasse zu Körpergrösse bei den Wirbeltieren. – Z. Morphol. Anthropologie, **18** (Festschrift G. A. Schwalbe), 323-350.

———, 1917: De maat der hersenen. Korte inhoud eener voordracht, gehouden op 18 Februari 1914. – Arch. Musée Teyler, Série 2, **3**, 282-294.

———, 1918a: De betrekking der hoeveelheden van de hersenen, het neuron en zijn deelen tot de lichaamsgrootte. – Versl. Kon. Akad. Wetensch. Amsterdam, **26**, 1416-1425.

———, 1918b: On the relation between the quantities of the brain, the neurone and its parts, and the size of the body. – Proc. Kon. Akad. Wetensch. Amsterdam, **20**, 1328-1337.

———, 1919a: De beteekenis der grootte van het neuron en zijn deelen. – Versl. Kon. Akad. Wetensch. Amsterdam, **27**, 503-520.

———, 1919b: The significance of the size of the neurone and its parts. – Proc. Kon. Akad. Wetensch. Amsterdam, **21**, 711-729.

———, 1919c: Vergelijking van het hersengewicht, in functie van het lichaamsgewicht, tusschen de twee seksen. – Versl. Kon. Akad. Wetensch. Amsterdam, **27**, 713-732.

———, 1919d: Comparison of the brain weight in function of the body weight, between the two sexes. – Proc. Kon. Akad. Wetensch. Amsterdam, **21**, 850-869.

———, 1920a: De hoeveelheidsbetrekking van de hersenen tot het lichaam der gewervelde diersoorten en hare beteekenis. – Vakblad Biologen, **1**, 82-89.

———, 1920b: De hoeveelheidsbetrekkingen van het zenuwstelsel bepaald door het mechanisme van het neuron. – Versl. Kon. Akad. Wetensch. Amsterdam, **28**, 623-638.

———, 1920c: The quantitative relations of the nervous system determined by the mechanism of the neurone. – Proc. Kon. Akad. Wetensch. Amsterdam, **22**, 665-680.

———, 1921: De beteekenis der groote schedelcapaciteit van Homo neandertalensis. – Versl. Kon. Akad. Wetensch. Amsterdam, **29**, 987-1004.

———, 1922a: On the significance of the large cranial capacity of Homo neandertalensis. – Proc. Kon. Akad. Wetensch. Amsterdam, **23**, 1271-1288.

———, 1922b: Phylogenetische en ontogenetische toeneming van het volumen der hersenen bij de gewervelde dieren. – Versl. Kon. Akad. Wetensch. Amsterdam, **31**, 307-332.

———, 1922c: Hat sich das Gehirn beim Haushunde, im Vergleich mit Wildhundarten, vergrössert, oder verkleinert? – Bijdragen Dierkunde, Afl. XXII (Feestnummer Max Weber), 315-320.

———, 1923: Phylogenetic and ontogenetic increase of the volume of the brain in Vertebrata. – Proc. Kon. Akad. Wetensch. Amsterdam, **25**, 230-255.

———, 1924a: Over de hersenhoeveelheid van gespecialiseerde zoogdiergeslachten. – Versl. Kon. Akad. Wetensch. Amsterdam, **33**, 319-326.

———, 1924b: On the brain quantity of specialized genera of Mammals. – Proc. Kon. Akad. Wetensch. Amsterdam, **27**, 430-437.

———, 1928a: De wet der noodwendige phylogenetische volmaking van het psychoencephalon. – Versl. Kon. Akad. Wetensch. Amsterdam, **37**, 252-259.

———, 1928b: The law of the necessary phylogenetic perfection of the psychoencephalon. – Proc. Kon. Akad. Wetensch. Amsterdam, **31**, 304-314.

———, 1930: Die phylogenetische Grosshirnzunahme autonome Vervollkommnung der animalen Funktionen. – Biologia generalis, **6**, 247-292. Vide: Corrigenda.

———, 1934a: Über die Gleichheit der Cephalisationsstufe aller Menschengruppen bei verschiedenem spezifischen Gehirnvolumen. – Biologia generalis, **10**, 185-193.

———, 1934b: Phylogenetic cerebral growth. – Congr. intern. sciences anthropol. et ethnologiques, Londres 1934. C.R. de la première Session, 71-75.

DUBOIS, E., 1938: Over de spronggrootte van den phylogenetischen en ontogenetischen hersengroei. – Vakblad Biologen, **20**, 37-46.

———, 1939: On insignificance of cranial vault-height in phylogenetic brain growth. – Proc. Kon. Akad. Wetensch. Amsterdam, **42**, 125-126.

FLOWER, W. H. & R. LYDEKKER, 1891: An Introduction to the Study of Mammals living and extinct. – London, Black, XVI + 763 pp.

FRANZ, V., 1934: Vergleichende Anatomie des Wirbeltierauges. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd II, 2. Hälfte, 989-1292. – Berlin & Wien, Urban & Schwarzenberg.

GAUPP, E., 1916: Das Schläfenbein und seine Darstellung im anatomischen, besonders im osteologischen Unterricht. – Archiv für Anatomie, Anatomische Abteilung des Archives für Anatomie und Physiologie, Jahrgang 1915 (1916), 62-105.

GÖPPERT, E., 1937: Kehlkopf und Trachea. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd III, 797-866. – Berlin & Wien, Urban & Schwarzenberg.

GREGORY, W. K., 1933: Fish Skulls. A study of the Evolution of Natural Mechanisms. – Transactions of the American Philosophical Society, New Series, **23**, Part II, I-VIII, 75-481.

GROEBBELS, F., 1932: Der Vogel. Bau, Funktion, Lebenserscheinung, Einpassung. Bd I: Atmungswelt und Nahrungswelt. – Berlin, Borntraeger, XII + 918 pp.

HALLER VON HALLERSTEIN, V., 1934: Äussere Gliederung des Zentralnervensystems. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Bd II, 1. Hälfte, 1-318. – Berlin & Wien, Urban & Schwarzenberg.

HOLMGREN, N. & E. STENSIÖ, 1936: Kranium und Visceralskelett der Akranier, Cyclostomen und Fische. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Bd IV, 233-500. – Berlin & Wien, Urban & Schwarzenberg.

KAMPEN, P. N. VAN, 1904: De tympanaalstreek van den zoogdierschedel. Thesis Univ. Amsterdam. – Amsterdam, XII + 379 pp.

———, 1905: Die Tympanalgegend des Säugetierschädels. – Morphol. Jahrbuch, **34**, 321-722.

KINGSLEY, J. S., 1925: The Vertebrate Skeleton from the developmental Standpoint. – Philadelphia, Blakiston, VIII + 337 pp.

KLAAUW, C. J. VAN DER, 1923: Die Skelettstückchen in der Sehne des Musculus stapedius und nahe dem Ursprung der Chorda tympani. – Z. gesamte Anatomie, 1. Abt. Z. Anatomie und Entwicklungsgeschichte, **69**, 32-83.

———, 1924: Bau und Entwickelung der Gehörknöchelchen. Literatur 1899–1923. – Ergebnisse der Anatomie und Entwicklungsgeschichte, **25**, 565-622.

———, 1931: The auditory Bulla in some fossil Mammals. With a general Introduction to this Region of the Skull. – Bull. Amer. Mus. Nat. Hist., **62**, 1-352.

———, 1941: Skelet van den kop. – In: J. E. W. Ihle, Leerboek der Vergelijkende Ontleedkunde van de Vertebraten. 2e druk, 223-282. – Utrecht, Oosthoek, X + 421 pp.

———, 1945: Cerebral Skull and facial Skull. A Contribution to the Knowledge of Skull-Structure. – Archives Néerlandaises de Zoologie, **7** (1946), 16-37.

LUBOSCH, W., 1938: Muskeln des Kopfes. Viscerale Muskulatur (Fortsetzung). B. Teleostier. C. Amphibien und Sauropsiden. D. Säugetiere. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd V, 1011-1106. – Berlin & Wien, Urban & Schwarzenberg.

LUTHER, A., 1938: Muskeln des Kopfes. Viscerale Muskulatur. Die Visceralmuskulatur der Acranier, Cyclostomen und Fische. A. Acranier, Cyclostomen, Selachier, Holocephalen, Ganoiden und Dipnoer. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd V, 467-542. – Berlin & Wien, Urban & Schwarzenberg.

MARINELLI, W., 1929: Grundriss einer funktionellen Analyse des Tetrapodenschädels (I. Mitteilung). – Palaeobiologica, Jahrgang II, **2**, Lief. 1-3. 128-141.

———, 1933: Die funktionelle Bedeutung der Postorbitalspange bei Giraffe und Pferd. – Biologia generalis, **9**, 2. Hälfte (Festschrift Versluys), 201-222.

———, 1936: Kranium und Visceralskelett. A. Allgemeine Probleme. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd IV, 207-232. – Berlin & Wien, Urban & Schwarzenberg.

———, 1936: Kranium und Visceralskelett der Sauropsiden, 2. Vögel. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Bd IV, 809-838. – Berlin & Wien, Urban & Schwarzenberg.

MATTHES, E., 1934: Geruchsorgan. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Bd II, 2. Hälfte, 879-948. – Berlin & Wien, Urban & Schwarzenberg.

MULLER, J., 1934: The orbitotemporal Region of the Skull of the Mammalia. – Archives Néerlandaises de Zoologie, **I** (1935), 118-259.

NISHI, S., 1938: Muskeln des Rumpfes. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd V, 351-446. – Berlin & Wien, Urban & Schwarzenberg.

———, 1938: Muskeln des Kopfes. Parietale Muskulatur. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd V, 447-466. – Berlin & Wien, Urban & Schwarzenberg.

NOBLE, G. K., 1931: The Biology of the Amphibia. – New York & London, McGraw – Hill, XIV + 577 pp.

OWEN, R., 1866 I: On the Anatomy of Vertebrates. Vol. I. Fishes and Reptiles. – London, Longmans, Green and Co., XLII + 650 pp.

———, 1866 II: On the Anatomy of Vertebrates. Vol. II. Birds and Mammals. – London, Longmans, Green and Co., VIII + 592 pp.

RAUBER–KOPSCH, 1922: Lehrbuch und Atlas der Anatomie des Menschen, Abt. 2: Knochen, Bänder. 12. Aufl. – Leipzig, Thieme, IV + 353 pp.

———, 1940: Lehrbuch und Atlas der Anatomie des Menschen, Bd I. 16. Aufl. – Leipzig, Thieme, IV + 645 pp.

STADTMÜLLER, F., 1936: Kranium und Visceralskelett der Stegocephalen und Amphibien. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Bd IV, 501-698. – Berlin & Wien, Urban & Schwarzenberg.

———, 1936: Kranium und Visceralskelett der Säugetiere. – In: L. Bolk,

E. Göppert, E. Kallius & W. Lubosch, Bd IV, 839-1016. – Berlin & Wien, Urban & Schwarzenberg.

Stratz, C. H., 1904: Das Verhältnis zwischen Gesichts- und Gehirnschädel beim Menschen und Affen. – Archiv für Anthropologie, N. F., **3**, 85-93.

Stresemann, E., 1927-1934: Aves. – In: W. Kükenthal, Handbuch der Zoologie, Bd VII, 2. Hälfte, Sauropsida: Aves. – Berlin–Leipzig, W. de Gruyter, xii + 899 pp. (1927: 1-224; 1928: 225-432; 1929: 433-544; 1931: 545-656; 1933: 657-768; 1934: 769-899).

———, 1937: Syrinx. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, Bd III, 867-882. – Berlin & Wien, Urban & Schwarzenberg.

Versluys, J., 1936: Kranium und Visceralskelett der Sauropsiden. 1. Reptilien. – In: L. Bolk, E. Göppert, E. Kallius & W. Lubosch, Bd IV, 699-808. – Berlin & Wien, Urban & Schwarzenberg.

Weber, M., 1927 I: Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. 2. Aufl., Bd I. – Jena, G. Fischer, xvi + 444 pp.

Williston, S. W., 1925: The Osteology of the Reptiles. – Cambridge, Harvard Univ. Press, xiv + 300 pp.

POSTWAR LITERATURE BY THE AUTHOR AND HIS SCHOLARS

E. Arendsen de Wolff-Exalto, 1951: On differences in the lower jaw of animalivorous and herbivorous mammals. I. II. Proc. Kon. Ned. Akad. Wetensch., Series C, **54**, 237-246, 405-410.

P. Dullemeijer, 1951: The correlation between muscle system and skull structure in *Phalacrocorax carbo sinensis* (Shaw & Nodder). I. II. III. Proc. Kon. Ned. Akad. Wetensch., Series C, **54**, 247-259, 400-404. No. III in the press.

M. Duym, 1951: On the head posture in birds and its relation to some anatomical features. I. II. Proc. Kon. Ned. Akad. Wetensch., Series C, **54**, 202-211, 260-271.

A. M. Husson, 1950: Some remarks on prognathism with special reference to the skull of *Pongo pygmaeus* (Hoppius). Proc. Kon. Ned. Akad. Wetensch., **53**, 199-210.

C. J. van der Klaauw, 1950: Architectuur van de schedel. Verslag Kon. Ned. Akad. Wetensch., **59**, 40-44.

V. Manger Cats, 1951: On the correlation between the muscles and the skull structure in the regio occipitalis and the regio otica of some Squaliformes. I. II. Proc. Kon. Ned. Akad. Wetensch., Series C, **54**, 191-201, 296-300.

M. C. A. Willemse, 1950: The shifting of the molar row with regard to the orbit in *Equus* and *Giraffa*. Zoologische Mededelingen, **30**, 311-326.

The following papers are in preparation:

by J. van den Assem on the attachment of muscles to the branchial skeleton in Squaliformes;

by H. L. Booy on the attachment of horns to the skull;

by P. D. Burggraaf on the attachment of muscles to the skull in *Phasianus*;

by J. A. G. Davids on the attachment of muscles to the skull in *Anas* and *Anser*;

by P. Dullemeijer a general paper on the attachment of muscles to the skull in *Phalacrocorax*;

by P. Fuchs on the attachment of muscles to the branchial skeleton in Squaliformes;

by A. M. Husson on size and shape of the foramen occipitale in *Pongo pygmaeus* (Hoppius);

by L. van Leeuwen on the attachment of muscles to the skull in *Sturnus* and *Turdus*;

by G. W. Versloot on the attachment of jaw muscles to the jaws in Squaliformes.

FIGURES ON PLATES AT THE END OF THE PAPER

Fig. 58 is printed on plate I.
Figs 59 a and b are printed on plate II.
Figs 70 a and b are printed on plate III.
Fig. 71 is printed on plate IV.
Fig. 110 a is printed on plate V.
Fig. 110 b is printed on plate VI.
Fig. 110 c is printed on plate VII.
Fig. 153 is printed on plate VIII.

ERRATA

On p. 40, line 5 from the bottom, read 1938, p. 37 instead of 1928, p. 37.

On p. 47, line 14 from the top, read p. 291 instead of p. 219.

On p. 149, line 4 from the top, read 1937 instead of 1933.

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COMPTES RENDUS DE LA SOCIÉTÉ NÉERLANDAISE DE ZOOLOGIE

JANVIER 1949—DÉCEMBRE 1950

Séance du 8 janvier 1949 à Leyde

1. J. DE WILDE (Amsterdam). Développement embryonnaire et post-embryonnaire du Doryphore (*Leptinotarsa decemlineata* Say) en fonction de la température.

Voir: Transactions VIIIth Intern. Congress of Entomology, Stockholm 1950.

2. P. D. NIEUWKOOP (Utrecht). Some new investigations concerning the determination of the central nervous system (in Amphibians).

Voir: Extrait du XIIIme Congrès Intern. de Zoologie, Paris, 21–27 juillet, 1948.

Séance du 12 février 1949 à Amsterdam

N. TINBERGEN (Leyde). Field work on animal behaviour, with slides and film.

Un résumé de cette conférence n'a pas été remis au secrétaire.

Séance du 12 mars 1949 à Utrecht

1. L. D. BRONGERSMA (Leyde). On the tracheal lung and lung in *Acrochordus* and some other snakes.

In the majority of snakes the left lung has become reduced to a mere rudiment or it has disappeared altogether. In a number of these species, belonging to widely different families a tracheal lung has developed, i.e., the dorsal wall of the trachea is covered by alveolar respiratory tissue. The various families and genera show differences in the structure of this tracheal lung. In the Viperidae the ligament that connects the dorsal ends of the tracheal cartilages has become much broadened, and this ligament bears the alveoli. Thus a tracheal lung is formed, the con-

tinuous lumen of which communicates with the lumen of the trachea over the whole of its length. In some species of the Viperidae the tracheal lung forms nearly the whole respiratory area; the lung itself has almost completely developed into a smooth-walled airsac.

In *Acrochordus* the situation is different. The tracheal lung does not have a continuous lumen that communicates with that of the trachea over the whole of its length. The tracheal lung of *Acrochordus* consists of two rows of sacs, which are attached to the dorsal surface of the trachea, and each of which opens into the lumen of the trachea through a separate pore. These pores are situated between the dorsal ends of the tracheal cartilages; the latter form almost complete rings, as their dorsal ends meet in the median line. The sacs are joined together by connective tissue, but their lumina do not communicate with one another. The inner surface of the sacs bears septs which divide them into alveoli. The septs show numerous capillaries close to their surface. The tracheal lung receives a branch of the pulmonary artery, and the blood is returned to the heart by a branch of the pulmonary vein.

The true lung of *Acrochordus* is well developed; it extends almost to the vent. It shows a narrow central canal, the wall of which is connected to the outer wall of the lung by radiating septs and by transverse septs. Thus the lung is divided into chambers each of which communicates with the central canal by a pore. The chambers are subdivided into alveoli by secondary septs. In the septs muscle fibres have developed. In the posterior part of the lung the septs are almost completely muscular (with numerous capillaries), and the posterior tip of the lung is also ensheathed by muscular tissue. The pulmonary artery and the pulmonary vein can be traced posteriorly over the whole length of the lung.

2. K. H. Voous Jr (Amsterdam). The postglacial dispersal of some arboreal bird species in Europe.

The subject has been discussed in the following publications:
On the distribution of *Garrulus glandarius brandti* Eversmann.
Voir: Limosa, **18**, 1945, p. 11–22.
On the history of the distribution of the genus *Dendrocopos*.
Voir: Limosa, **20**, 1947, p. 1–142.
Distributional history of Eurasian Bullfinches, genus *Pyrrhula*.
Voir: The Condor, 1949.

Séance du 7 mai 1949 à Oosterbeek à l'Institut des recherches biologiques appliquées dans le milieu naturel

1. A. D. VOÛTE (Oosterbeek). Exposition générale des recherches de l'Institut.

2. J. VAN DER DRIFT (Oosterbeek). La faune du sol des forêts. Voir: Tijdschrift voor Entomologie, **94**, 1951.

3. E. T. G. ELTON (Oosterbeek). *Dendroctonus micans* Kug. un ennemi de *Picea sitchensis* aux Pays Bas.
Voir: Transactions VIIIth Intern. Congress of Entomology, Stockholm 1950.

4. J. A. EYGENRAAM (Oosterbeek). Le dynamisme de la population du Coq de bruyère.
Voir: T. N. O. Nieuws, **5**, no. 50, 1950.

Séance du 22 octobre 1949 à Leyde

1. I. KRISTENSEN (Den Helder). L'influence des températures sur la faune le long de notre côte.
Cette conférence sera publiée, à titre modifié, dans les Archives Néerlandaises de Zoologie.

2. M. DUYM (Groningue). Sur quelques aspects du port habituel de la tête chez les oiseaux.
Voir: Proceedings Kon. Ned. Akad. Wet. (C), **54** (1951), p. 202-211; 260-271.

Séance du 22 décembre 1949 à Amsterdam

1. H. P. WOLVEKAMP, L. DE RUITER et A. J. VAN TOOREN (Leyde). Expériences sur la respiration de quelques insectes aquatiques: *Hydrous piceus* L, *Naucoris cimicoïdes* L et *Notonecta glauca* L.
La conception de COMSTOCK et de KROGH et l'interprétation que EGE donne à ses expériences (que les provisions d'air que plusieurs insectes aquatiques emportent en plongeant sous la surface de l'eau, ne servent pas seulement de réserves d'oxygène mais aussi

d'organes respiratoires) a été confirmée pour *Naucoris* et *Notonecta*. Ce sont des insectes qui produisent un courant d'eau le long des surfaces de leur bulle d'air à l'aide de la dernière paire de pattes. La signification de ces mouvements de ventilation se démontre par l'abaissement considérable de la consommation d'oxygène lorsque les pattes postérieures sont immobilisées. Dans ce cas la diminution de la consommation d'oxygène n'est pas causée par une réduction des besoins métaboliques, mais la respiration est limitée par la diffusion, puisque la consommation d'oxygène se relève aussitôt que l'animal est mû dans l'eau.

Les mouvements respiratoires sont excités par le CO_2, tandis que des tensions d'oxygène diminuées portent les deux espèces citées plus haut à renouveler leurs provisions d'air.

Hydrous ne fait pas de mouvements respiratoires et c'est comme ça que doit être expliqué le fait remarquable que la quantité d'oxygène absorbée du milieu aquatique (exprimée en $cm^3/k./h.$) est aussi négligeable que dans le cas de *Dytiscus*, quoique la surface de la bulle d'air soit beaucoup plus étendue dans le cas d'*Hydrous* que dans celui du Dytique.

A des températures élevées (15–20°) la quantité d'oxygène extraite de l'eau ne forme qu'une fraction de la consommation totale d'oxygène. A des températures basses (4–5°) *Naucoris* et *Notonecta* sont capables de couvrir leur besoin d'oxygène par la seule respiration aquatique, ce qui confirme l'opinion exprimée par Ege.

2. J. W. Sluiter (Aussi de la part de G. J. van Oordt et J. C. A. Mighorst) (Utrecht). A study of the testis tubules, interstitial tissue and sex characters (thumb-pads and wolffian ducts) of normal and hypophysectomized Frogs (*Rana esculenta*).

Voir: Quart. Journ. Microsc. Sc., **91**, part 2, June 1950.

Séance du 14 janvier 1950 à Utrecht

1. C. O. van Regteren Altena (Leyde). The Limacidae of the Canary Islands.

Voir: Zool. Verh. Rijksmus. v. Nat. Hist., **11**, déc. 1950.

2. M^elle^ B. Baggerman (Leyde). La combinaison d'oxygène et de CO_2 avec le sang du Crabe *Cancer pagurus* L.

On a déterminé les courbes de dissociation de l'oxygène dans le sang du Crabe à des pressions partielles différentes de CO_2 (selon la méthode de PANTIN et HOGBEN) et les courbes d'absorption de CO_2 (selon les méthodes gasométriques usuelles). On a déterminé le pH des échantillons à l'aide de l'électrode de verre.

La position des courbes de dissociation de l'oxyhémocyanine ne différait que fort peu de celle des courbes déterminées par Mme et M. STEDMAN et par WOLVEKAMP. L'effet BOHR était beaucoup plus faible que dans le cas du Homard (WOLVEKAMP).

La composition des échantillons du sang divergeait considérablement, fait prouvé par les variations du pouvoir tampon.

Donné le même pH, la position des courbes de dissociation se déplaçait vers la droite à mesure que le sang était plus dilué. Il n'a pas été possible de constater si cet effet devait être attribué à l'influence des concentrations différentes des sels et/ou à celles de l'hémocyanine même.

A l'heure qu'il est, il n'est pas possible de constater un rapport biologique entre les propriétés respiratoires du sang, les conditions du milieu extérieur et l'activité fonctionnelle de l'animal.

3. J. C. VAN DE KAMER (Utrecht). On the function of the pineal organ.

Prior to its function the morphology of the pineal organ was treated and its localization at the roof of the brain, in different groups of Vertebrates. Then the functional theories were critically analysed. The following possibilities were discussed:

1. the pineal organ is a gland.
2. the pineal organ is an endocrine gland; its function is to suppress the development of the gonads.
3. the pineal organ is related to metamorphosis.
4. the organ is in reduction and has no special function.
5. the organ is sensitive to light.
6. the organ is a sense organ, the function of which is to measure the pressure of the cerebral fluid or to sense the chemical constitution of this fluid.

Different objections were raised against the first five possibilities. The last possibility is most likely the best, since in the pineal organ of *Petromyzon*, *Acanthias*, the "Stirnorgan" of Anura and in the pineal sac of Reptiles sense cells are present. Sense cells were also found by the author in the pineal organ of Anura,

Urodela, Birds and Mammals. In addition, in Fishes, Amphibia, Reptiles and Birds the organ has a cavity, which is in open communication with the brain cavity, and is most often situated under the cranium or covered by pigment.

Experiments must give conclusive evidence of the function of the sense cells and more morphological and cytological details must be gathered on the pineal organ in the different groups of Vertebrates.

Séance du 11 février 1950 à Amsterdam

P. J. Gaillard (Leyde). Manifestations de croissance et développement des cultures de tissue.

Les phénomènes discutés ont été publiés dans les journaux suivants:

Developmental changes in the composition of the body fluids in relation to growth and differentiation of tissue cultures.

Voir: Protoplasma, Bd. XXIII, Hft. 2, 1935.

Gesetzmässigkeiten beim Wachstum von Gewebekulturen I: Analyse der Zellteilungsfrequenz.

Voir: Protoplasma, Bd. XXIV, Hft. 3, 1935.

Gesetzmässigkeiten beim Wachstum von Gewebekulturen II: Analyse der Zellbewegung.

Voir: Protoplasma, Bd. XXV, Hft. 4, 1936.

Hormones regulating growth and differentiation in embryonic explants (Monographie).

Voir: Act. Sci. et Industr. Paris. no. 923, 1942.

The growth of explanted embryonic cells.

Voir: Acta Neerlandica Morphologiae Normalis et Pathologicae. Extr. ex vol. VI, no. 1/2, 1948.

Growth, differentiation and function of explants of some endocrine glands.

Voir: Symposia of the Soc. f. Exp. Biology, no. II: Growth in relation to differentiation and morphogenesis, 1948.

Sex cell formation in explants of the foetal human ovarian cortex I.

Voir: Proc. Kon. Ned. Akad. v. Wetensch., LIII, no. 8, 1950.

Sex cell formation in explants of the foetal human ovarian cortex II.

Voir: Proc. Kon. Ned. Akad. v. Wetensch., LIII, no. 9, 1950.

Séance du 18 mars 1950 à Leyde

1. L. K. Boerema. On the ethology of the Grayling, *Eumenis semele* L.

The courtship of the Grayling consists of a series of different reactions. The male flies towards a passing female and follows her. If the female responds she settles on the ground. The male alights in her neighbourhood and walks towards her. He then performs a series of four different movements in front of the female, until copulation results. The female does not move during this performance.

The courtship on the ground has been analysed with dummies. It appeared that each movement of the male is released by a different set of stimuli from the immobile female. This means that the stimuli for each movement are continually present. Still the male generally keeps to the usual sequence. I never succeeded in releasing e.g. the third movement by presenting a dummy which only possessed the stimuli for this movement in a male which was not already courting up to this stage. A first attempt for an interpretation of this phenomenon has been given in this paper.

2. J. Hofker (La Haye). Alterations in phaenotype of Foraminifera from successive geologic horizons and suppression of generations in the reproductive cycle which may have caused those alterations.

When studying *Buliminae* from the Tertiary of the Netherlands I found that *Bulimina elongata* d'Orbigny from the Oligocene and lower Miocene possesses a simple toothplate and forms no outer spines as ornamentation. The species is trimorphic. In the Middle Miocene a new species develops, recognisable by its somewhat more ornamented toothplate with respect to that of *B. elongata.* I identified it with *Bulimina echinata* d'Orbigny, though the types in the lower part of the Middle Miocene show no spines whatever, especially so in the microspheric generation. Here the species also is trimorphic. In the upper layers of the Middle Miocene this species forms at its initial end distinct spines and has been regarded by several authors as *B. aculeata* d'Orbigny; comparison with topotypes, however, revealed that the latter species shows a quite different toothplate. Simultaneously with the development of spines in Miocene *B. echinata* the mode of reproduction alters;

whereas the spineless form from the lower Middle Miocene is trimorphic, the A_2-generation in the spinous form of the upper Middle Miocene falls out and in the typical forms of the upper layers even the B-generation is missing. The spinous form has become apogamic.

A quite similar reduction of the reproductive cycle is found in the Tertiary species *Asterigerina gurichi* (Franke). In the Middle Oligocene three generations occur, B, A_1 and A_2; in the upper part of the Middle Oligocene the A_2-generation which shows very typical supplementary chambers, disappears, and in the Miocene only the A_1-generation is left. At the end of the Middle Miocene the species has vanished. As the three generations of *A. gurichi* show minor differences, it was supposed that one could distinguish three different species, characteristic for three different geologic ages; my investigations on a very large material show me, however, that these three "species" are the three generations; in the older geologic times all three generations occur; then A_2 disappears, and later on also the B-generation.

As I could prove that a similar phenomenon can also be shown in several species of Cretaceous age, this discovery seems to be of very valuable significance, especially for stratigraphic purposes. So I worked out a method for analysing the reproductive cycle in fossil Foraminifera, which method consists in measuring the length (or diameter) of the whole test, and dividing this figure by the total number of chambers in the test. As this quotient is quite typical for the different generations, one obtains very clear diagrams when comparing this quotient with the diameter of the proloculus of each test. I could compare my results with diagrams obtained from recent species of which the scheme of reproduction is known already.

Symposium sur l'évolution des êtres organisés du 19–20 mai 1950 à Utrecht

1. H. J. Lam (Leyde). Introduction au problème de l'évolution.

L'évolution dans son sens le plus large est le problème de tout changement, mais il est limité ici au changement des organismes sur la terre. Le temps est le facteur le plus apparent et il est difficile de trouver la relation entre les changements observables pendant quelques générations humaines et ceux révélés par la paléontologie stratigraphique.

L'auteur part de la thèse que l'évolution va du moins différencié au plus différencié. Selon lui la vie n'est apparue sur terre qu'en une seule période de son refroidissement. La forme la plus simple de la vie n'existe plus ou n'est, du moins, pas encore découverte.

Suit un aperçu de l'historique de l'évolution.

En 1949 parut sous la rédaction de JEPSEN, SIMPSON et MAYR un ouvrage synthétique sur l'évolution ("Genetics, Paleontology and Evolution"). Il est significatif que malgré les grandes qualités des auteurs, la coördination entre paléontologistes, systématiciens, écologistes et généticiens n'a pas abouti à un succès. Aucun des collaborateurs n'est parvenu à s'assimiler suffisamment les autres disciplines.

L'étude actuelle de l'évolution gravit encore autour des deux pôles: génétique-cytologie et paléontologie.

La génétique nous a appris que tous les noyaux, non seulement ceux des gamètes, sont porteurs de propriétés héréditaires et que les gènes sont organisés d'une manière linéaire dans les chromosomes, bien que parfois on en rencontre en dehors du noyau.

La relation gène propriété est très complexe. Puisque un seul caractère peut être déterminé par plus d'un gène et qu'un seul gène influence souvent plus d'un caractère on peut parler de relations biochimiques réticulaires entre les gènes et les caractères.

Dès qu'on admet que les organismes inférieurs ont moins de gènes que les organismes supérieurs, il faut admettre un ou plusieurs gènes primitifs, qui seraient à l'origine de tous les autres.

Les gènes nous apparaissent comme des molécules d'une substance protéinique très stable. Les mutations consisteraient en des sauts d'énergie. Ils se manifestent comme des changements de caractères constants.

Les mutations expérimentales et spontanées sont de même nature mais la cause de ces dernières est inconnue.

Le degré de mutations spontanées est minime: 10^{-5} à 10^{-6} par gamète par génération. A cause des relations entre gènes et caractères le degré de mutation des caractères est beaucoup plus grand: 10^{-4} à 10^{-2} par génération. Il existe une relation simple mais en raison inverse entre la durée des générations et la vitesse de l'évolution.

La plupart des mutations spontanées sont nocives: les grandes plus que les petites. Les mutations sont spécifiques, aussi dans ce sens qu'elles sont déterminées aussi par leur génome.

Il y a une pression de mutation. La pression de sélection du milieu en forme la force antagoniste. Entre les deux se trouvent individus et groupes d'individus (communautés d'hybridisation) en un équilibre plus ou moins instable. Leur plasticité est la base de l'évolution. Cette plasticité à cause du génome, a une préférence pour certaines directions (mutations favorisées).

La sélection par le milieu porte surtout sur les communautés d'hybridisation à plasticité maximale et plus spécialement sur des petits groupes reposant sur de petites différences de génome ou de milieu. Les divergences s'accentuent jusqu'à ce que les différences amènent l'impossibilité d'hybridisation et d'échange de gènes. Ce phénomène peut avoir une base ou subir une influence génétique, écologique, psychique ou géographique. De cette façon apparaissent évidemment ce qu'on appelle les "grandes" espèces.

Chaque unité systématique ou "taxon" est réelle et chaque possède son propre histoire. La hiérarchie de ces unités en des catégories qui s'enveloppent mutuellement est oeuvre humaine. Si la continuité naturelle est interrompue, cela est dû à des procès de désagrégation qui deviennent dominants aussitôt que les groupes ne peuvent plus échanger de gènes. Ceci concorde avec la corrélation entre l'âge et le rang (ou la grandeur) des unités, démontrée par la paléontologie, mais ne nous explique guère comment un niveau plus élevé est atteint.

La paléontologie nous montre des changements de caractères. Ceux-ci se laissent raccorder en séries phylogénétiques et lorsque ces séries passent d'un taxon à un autre, il faut en conclure qu'il existe une potentialité générale ayant dans les divers groupes une part différente. Seule la paléontologie peut nous révéler ce qui est primitif et ce qui est secondaire.

La phylogénie des groupes ne nous est pas révélée par la paléontologie. L'élément subjectif y est encore plus important que dans la phylogénie des caractères. Ce qu'on appelle la phylogénie d'un groupe n'est souvent en réalité qu'une affinité supposée.

Les orthogénèses si imposantes de la paléozoölogie, ne sont pas si continues qu'on le croirait à première vue. Pourtant elles reposent certainement en partie sur des orientations génomatiques. Les paléontologistes sont enclins à surestimer ces orientations, les généticiens pourraient les sousestimer. La plupart de ces derniers voient dans l'évolution un phénomène en grande partie indéterminé. Peut-être des méthodes de chronologie stratigraphique raffinées peuvent concilier les deux extrêmes.

L'évolution de l'homme, à part quelques recherches génétiques, est le fait des paléontologistes et des archéologues. Les généticiens voient dans le *Homo sapiens* une espèce sans possibilité de sélection externe, qui commence à devenir un danger pour elle-même. Ils espèrent une sélection intellectuelle, une "biological engineering" qui pourrait remplacer la sélection naturelle.

Les paléontologistes comptent sur l'orthogénèse acceptée, et s'attendent à une domination toujours plus importante de l'esprit. L'auteur voit dans le polymorphisme de ce qui semble devenir bientôt une seule communauté d'hybridisation la possibilité d'un niveau plus élevé.

De nos jours l'étude de l'évolution connaît donc beaucoup de détails, mais l'élément d'union manque encore: il nous manque la compréhension de l'origine des mutations, du rapport entre génome et milieu, du lien entre génétique et taxogénèse et du lien entre la phylogénie des caractères et celle des groupes. Cependant, la suggestion s'offre que la solution du problème se trouvera dans le domaine de la nature de la matière et de la vie. L'omnivalidité de la causalité, contestée par les microphysiciens, pourrait alors être révisée dans un ordre supracausal.

2. M. J. SIRKS (Groningue). L'Aspect génétique de l'évolution.

Les hommes de science, et en tout premier lieu ceux qui s'occupent de la biologie, ne sont pas assez scrupuleux parfois dans leurs modes d'expression; leur idiome ne satisfait pas toujours les exigences. Preuve de cette thèse se trouve par exemple dans le fait, qu'on a pris l'habitude de parler d'un *problème* de l'évolution, tandis que personne ne saurait expliquer le contenu de ce problème. Il est vrai, nous rencontrons dans la nature le *phénomène* de l'évolution du règne vivant, mais on néglige le fait que ce phénomène nous présente nombre de problèmes de caractères très variés. Cette confusion a abouti, il y a une vingtaine d'années encore, à deux pôles opposés. Le Professeur HONING, professeur de génétique à l'Ecole Supérieure d'Agriculture de Wageningen, dans son discours d'inauguration en 1920 a défendu la thèse que les généticiens ne soient pas intéressés aux phénomènes de l'évolution, vu qu'ils ne pourraient aucunement contribuer à l'explication de ce phénomène, point de vue trop sceptique à mon avis. D'autre part les paléontologues, optimistes, en considérant les phénomènes de l'évolution comme une entité, ont été d'opinion qu'on saurait résoudre le tout par des conclusions, basées sur leurs observations, en niant la valeur et même la nécessité d'une base exacte, fournie par l'expérimentation. Pour illustrer cette attitude, je mentionne une boutade du professeur BROOM, le paléontologue sudafricain, bien connu pas ses études sur les formes ancêtres de l'homme. En visitant son musée avec un groupe de biologistes néerlandais, il s'est adressé à moi en disant: "My friend here, the geneticist, thinks he *may* tell you how evolution *may* have happened, but we as paleontologists, *can* tell you how it *did* happen".

Cette antithèse d'un scepticisme chez les généticiens et d'un optimisme exagéré chez les paléontologues, est en train de disparaître; les généticiens ont compris que leur science aussi peut contribuer pour leur part quelque chose à l'explication du phénomène de l'évolution, les paléontologues ont reconnu qu'il faut épurer leurs conclusions par la critique plus exacte des biologistes expérimentaux.

Cette antithèse a été reconnue telle par PHILIPTCHENKO (1927, p. 94) qui en a démêlé les principes d'une micro-évolution et d'une macro-évolution. La micro-évolution nous offre des problèmes de caractère génétique et s'occupe avant tout de la naissance de biotypes, jordanons et linnéons, de toutes les distinctions taxonomiques de l'espèce et de ses composants. La macro-évolution étude par l'observation l'évolution des groupes taxonomiques de rang supérieur, c.à.d. au-dessus de l'espèce. Cette distinction a beaucoup contribué à éclaircir la structure du phénomène de l'évolution. Récemment, SIMPSON (1944, p. 98) a ajouté le terme de méga-évolution: la macro-évolution s'occupant de groupes taxonomiques du rang d'espèces et de genres, la méga-évolution étudiant l'évolution sur une grande échelle, celle des familles, classes, ordres et phyla. On pourrait comparer les micro-évolutionnistes à des fourmis, qui rassemblent beaucoup de matériel à la campagne; les macro-évolutionnistes regardent les phénomènes de l'évolution du point de vue d'un aigle, qui nous sait décrire les apparences superficielles du terrain, sans aucune connaissance de la structure géologique ou chimique des montagnes et des plaines. Ou bien les micro-évolutionnistes considèrent le phénomène de l'évolution à deux dimensions, les macro-évolutionnistes vivent dans un monde de quatre dimensions. Cependant le phénomène de l'évolution se trouve entre ces deux extrêmes; son monde est celui de trois dimensions. SIMPSON craint que les généticiens ne courent risque d'une myopie; c'est vrai, mais alors il faut dire que les paléontologues en quelque sorte souffrent d'une hypermétropie.

Pour trouver en fin de compte l'explication de tout le phénomène de l'évolution il faut analyser ce phénomène dans ses éléments composants, et dès qu'on aura appliqué cette analyse, il en résout immédiatement que chaque élément représente un problème spécial, que le prétendu problème de l'évolution contient tout un assemblage de problèmes de caractères bien différents. Une analyse provisoire des phénomènes de l'évolution nous amène les questions divergentes:

1. Quelle est la cause de la naissance d'un individu à génotype différent de celui de ses parents?
2. Quelle peut être la portée d'action d'un seul gène?
3. Quelle est la destinée d'un individu à génotype changé et de sa postérité, parmi le groupe d'individus, disons population, parmi laquelle il a pris naissance?
4. Quelles sont les causes, qui influencent la composition d'une population, de sa structure génotypique, et la formation de nouvelles populations?
5. Quelles sont les causes de l'évolution en sens pure, c.à.d. du phénomène que la structure anatomique des organismes pendant les époques de la terre devient de plus en plus compliquée?

Ad 1. Il va de soi que la première question est de nature purement génétique. DARWIN de son temps n'a pas su résoudre cette question, et même dans son livre cette question est restée plus ou moins dans l'ombre. Sa réponse a été indécise, quelque peu Lamarckienne. A présent nous disposons de nombre de réponses: mutation de gène, mutation chromosomique, mutation du génome, mutation du plasme, hybridisation. Mais néanmoins le problème reste actuel, faute de données incontestables et irréfutables. Une critique sévère nous relève des objections. Les mutations de gènes, bienque fréquemment obtenues sous des conditions artificielles, sont assez rares dans la nature et leur origine nous reste voilée. La portée d'action d'un seul gène est généralement considérée trop restreinte pour qu'une mutation d'un seul gène ne puisse beaucoup contribuer à l'évolution. Les mutations chromosomales et celles du génome ne produisent pas un gain de nouveaux gènes, mais seulement une perte, une réduplication, un changement de position. Les hybridisations, sans doute cause d'une origine explosive de recombinaisons de gènes, ne produisent pas de nouveaux gènes; en outre la plupart des taxonomistes contestent que le processus d'hybridisation joue un rôle d'importance dans la nature.

Toutes ces objections sont valables à un certain degré, mais tout de même il faut admettre que la génétique a prouvé l'importance des mutations et le rôle de l'hybridisation comme sources de naissance d'organismes nouveaux. Il faut admettre également, bien que comme hypothèse, un interchange d'éléments entre deux gènes différents comme source d'un nouveau gène. Et en outre il ne faut pas oublier que ce n'est pas le gène comme tel qui compte, mais le génotype en total, la collection de gènes à disposition pour un organisme. Bien qu'elle n'ait pas encore définitivement résolu ce problème, la génétique a commencé à en éclaircir le caractère fondamental et la solution de ce problème appartient somme toute à la génétique.

Ad 2. Le mendélisme primitif a montré que les caractères morphologiques, comme les couleurs et les formes des organes, sont causés par des gènes. Depuis on a pu constater que la portée d'action de gènes s'étend non seulement aux caractères physiologiques, mais encore à la création d'organes et à leur fonctionnement. La différence entre les Souris normales et la race naine dépend d'une seule paire d'allèles; l'allèle dominant causant la production des cellules éosinophiles dans l'hypophyse, laquelle est en défaut chez les Souris naines. La formation de la glande de WEISMANN, corpora allata, responsable de la nymphose des Drosophiles, dépend d'un seul gène. L'absence du chorda dorsalis dans le brachytype des Souris à queue raccourcie est le résultat de l'absence d'un seul gène. Les déficiences de chromosomes X dans la Drosophile, décrite par POULSON (nullo-X, déficience XR, déficience XL et Notch-8) forment toute une série de dérangements dans le développement larval: dans le type nullo-X (sans chromosome X), la moitié de la blastule se développe normalement, le reste dégénère; dans la déficience du bras droit du chromosome X (XR) la partie normale de la blastule est étendue, mais le blastoderme reste incomplet; la déficience du bras gauche (XL) du chromosome X permet la formation d'un blastoderme complet, mais après quatre heures de développement (formation du proctodaeum) le développement est interrompu et les tissus initiaux commencent à dégénérer; la déficience Notch-8 (une petite partie, les bandes 3C1-3D6 du chromosome X font défaut) se développe normalement pendant 8 heures, mais depuis on constate des phénomènes de dégénérescence. On connaît nombres de facteurs létaux, qui dans leur nature homozygote récessive causent une cessation d'un développement quelconque, mais on est incliné à négliger la conclusion parallèle, c'est que le facteur dominant est responsable de la formation d'un organe qui élève l'organisme à un plan supérieur. Toutes ces données justifient la thèse, qu'un nouveau gène ou une nouvelle combinaison de gènes peut jouer un rôle suffisamment important pour expliquer plusieurs des étapes considérables, que nous rencontrons dans le phénomène de l'évolution. Pour cette étude, la génétique peut nous fournir les matériaux de construction, mais c'est la physiologie du développement qui nous explique l'action des gènes.

Ad 3. La destinée d'un individu à génotype changé et de sa postérité dépend de nombre de facteurs essentiels, en premier lieu du caractère dominant ou récessif du nouveau gène. On est incliné à admettre qu'un gène nouveau dominant aille se répandre parmi la population comme une goutte d'huile sur l'eau, mais des calculs simples nous montrent que ceci ne se passe pas, à moins que l'activité de ce gène ne fournisse pas d'avantages aux individus changés en génotype. Bien que nous disposons d'une littérature mathématique riche sur ce problème (formule de HARDY, FISHER, HALDANE, WRIGHT), il me semble qu'on exagère l'importance de ces calculs du point de vue génétique et évolutionniste, vu le fait qu'on considère seulement le mode de reproduction (autogamie ou allogamie), tandis qu'on néglige les circonstances accessoires, d'une importance essentielle, savoir toutes les différences en vitalité, fécondité, fertilité causées par les gènes, qui peuvent jouer un rôle dans la sélection naturelle.

Ad 4. L'étude du dynamisme des populations, origine des espèces en sens stricte, est fondée sur notre connaissance de la géographie des gènes, science concentrée issue de la biogéographie. Ce dynamisme dépend de plusieurs facteurs inhérents et presque toujours fondés dans le génotype: mode de reproduction, vitalité, intensité de reproduction (précocité, durée de la période d'activité sexuelle, fécondité, fertilité, accouplement préférentiel), mais aussi de causes de conditions extérieures (milieu, climat, etc.; isolation géographique et isolation de saison). J'ai discuté ce problème dans une conférence antérieure (1949); c'est pourquoi je me borne à ce bref résumé.

Ad 5. La question finale de l'évolution c'est à expliquer les causes du phénomène que la structure anatomique des organismes pendant les époques de la terre devient de plus en plus compliquée.

Je suis obligé d'avouer que la réponse à cette question se trouve jusqu'ici hors d'atteinte en cequi concerne la génétique et qu'il faut disposer de l'optimisme des paléontologues pour nous offrir une solution suggestive et acceptable, même spectaculaire, mais . . . sans preuve.

LITTÉRATURE.

HONING, J. A., 1920. Erfelijkheidsleer zonder evolutietheorieën (Wageningen: Veenman, 1920: 16 pp.).

PHILIPTSCHENKO. J., 1927. Variabilität und Variation (Berlin: Borntraeger, 1927: 101 pp.).

SIMPSON, G. G., 1944. Tempo and mode in evolution (New York: Columbia Univ. Press, 1944: 237 pp.).

SIRKS, M. J., 1949. De dynamiek van populaties (Natuurwetensch. Tijdschr., Gent, **31**: pp. 227–242). Le dynamisme des populations(Acad. Int. Philos. des Sciences, sous presse).

3. G. VANDEBROEK (Louvain). Les données embryologiques nouvelles et la classification générale des Metazoaires.

Des données embryologiques nouvelles, dont plusieures sont connues déjà depuis quelques années, montrent, que la position systématique de certains groupes des Metazoaires, selon la classification en usage, n'est plus d'accord avec les faits actuels.

La gastrulation des Entéropneustes, Echinodermes et Chaetognathes – réunis dans cette conférence-ci sous le nom de Cycloneuriens – est absolument différente de la gastrulation des Chordés aussi bien que des Protostomes.

Suivant cette idée, il est impossible de grouper les Cycloneuriens avec les Chordés sous le nom de Deuterostomes. Le groupement des Cycloneuriens avec les Protostomes sous le nom d'Evertébrés est encore plus contradictoire aux données reconnues.

La connaissance de l'organisation des embryons conduit aux mêmes conclusions.

Entre les groupements des Echinodermes d'une part et des Protostomes d'autre part, il n'existe aucune relation; cependant on trouve bien une affinité entre les Protostomes et les Chordés.

Par conséquence, il est recommandable de grouper les Protostomes et les Chordés sous le nom de Ténoneuriens.

4. K. H. Voous (Amsterdam). La zoogéographie et l'évolution.

Les travaux de Kleinschmidt, Rensch, Huxley et Mayr ont mis en évidence les rapports entre la zoogéographie et l'étude de l'évolution organique. Le point de départ de ce genre d'études est l'espèce polytypique, représentée par une mosaïque de races localisées géographiquement (sous-espèces).

La formation de l'espèce ("spéciation"), qui est un des phénomènes les plus marquants de la zoogéographie peut être: 1) un changement de l'espèce dans le temps, aussi bien que: 2) une augmentation de l'espèce dans l'espace; les deux vont de pair.

Les seules unités à étudier par les zoogéographes sont constituées par les populations; celles-ci sont des communautés de multiplication locales, vaguement limitées. Les recherches génétiques et morphologiques des populations doivent contribuer à la détermination scientifique de la mosaïque actuelle d'une espèce.

L'apparence phénotypique d'une population est déterminée par au moins 4 facteurs: 1) la densité de la population; 2) la sélection naturelle; 3) la valeur adaptative des propriétés variables; 4) le coefficient de mutation. Ces facteurs acquièrent par l'isolement géographique une valeur différente, spécifique pour chaque localisation, de sorte que des changements dans la garniture génétique totale se produisent. Des exemples démontrent l'isolement de reproduction entre populations par l'isolement géographique. C'est le premier pas vers l'augmentation de l'espèce dans l'espace.

De nos jours, on s'intéresse beaucoup à l'adaptation écologique de populations isolées qui favorise l'isolement de reproduction. Il semble que l'isolement écologique est toujours de nature micro-géographique et que les limites entre l'isolement micro-géographique et macro-géographique sont toujours artificielles, bien que souvent très évidentes. De plus il semble que l'apparition d'un groupe d'individus à caractères écologiques spécifiques est beaucoup moins important que le maintien de toute une population écologique. Dans ce cas le degré d'isolement géographique